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SILICIFIED PRODUCTOIDS FROM THE VISEAN OF COUNTY FERMANAGH

BY

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SILICIFIED PRODUCTOIDS FROM THE VISEAN OF COUNTY FERMANAGH

By C. H. C. BRUNTON

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I. SYNOPSIS

Visean limestones exposed to the south-west of Lower Lough Erne in county Fermanagh, Northern Ireland, have yielded a silicified fauna rich in brachiopods and bryozoans. The brachiopods will be described in a series of papers of which this is the first and deals with the productoids. Fourteen genera are represented including 4 new species. The Strophalosiidae are believed to be the first recorded from the Lower Carboniferous rocks of the British Isles. Heteralosiinae is placed into junior synonymy with Strophalosiinae and a new subfamily,

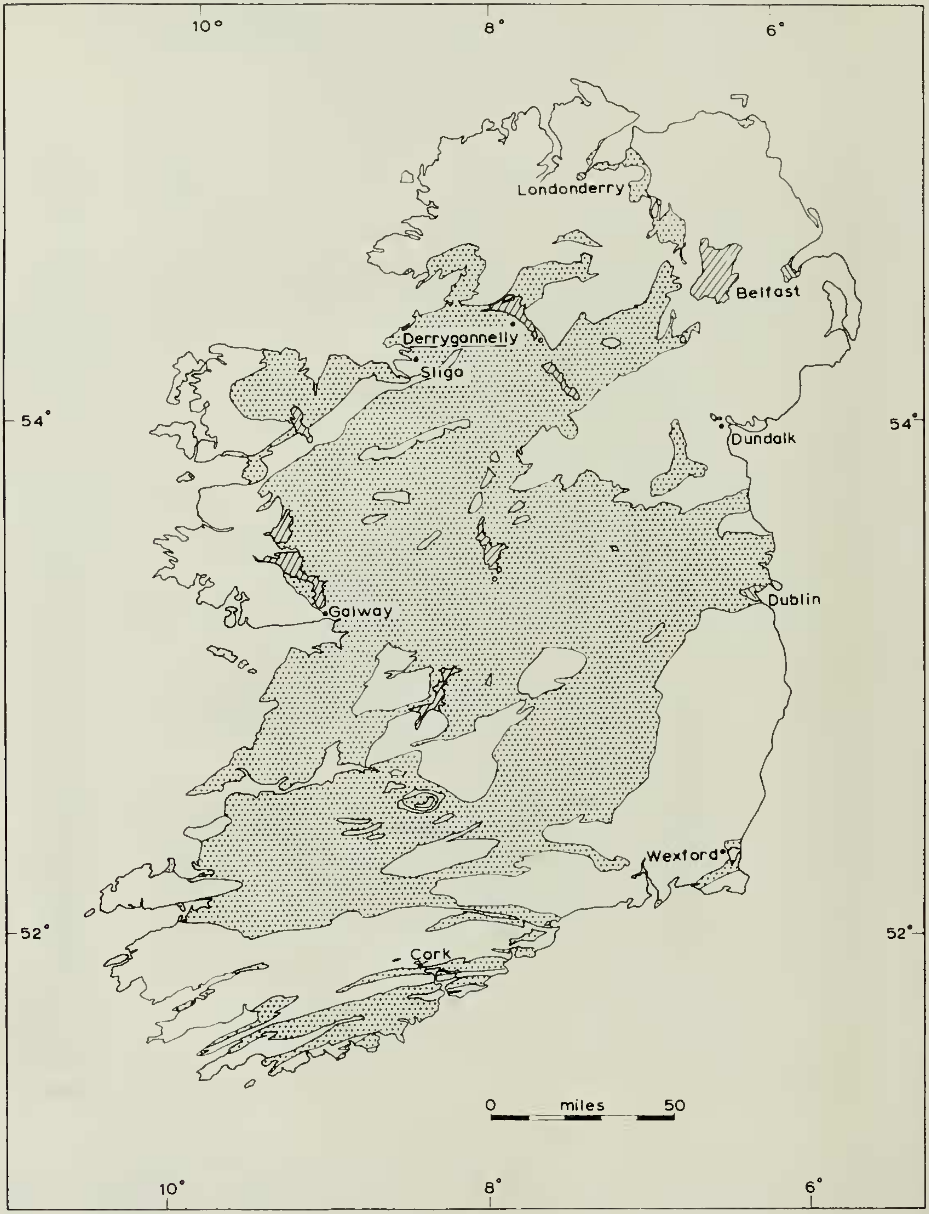

FIG. 1. Map of Ireland showing the position of Derrygonelly, from near which the faunas were collected, in relation to the Carboniferous rocks (dotted).

Dasyalosiinae, is erected for completely spinose strophalosiids. Juvenile shells have revealed structures indicating a closer relationship between the productoids and chonetoids than is commonly accepted.

II. INTRODUCTION AND ACKNOWLEDGMENTS

Despite being the area from which Phillips collected several of the type specimens described in his work of 1836, county Fermanagh has received little geological attention until recent years. The area from which the author has made faunal collections lies to the south of Lower Lough Erne, about 12 miles west-north-west of Enniskillen and close to Bunnahone and Carrick Loughs. A prominent crescent of hills composed of chert bearing or reefal limestone, generally identified as the Dartry Limestone group, forms a topographic feature throughout the counties of Sligo, Leitrim and Fermanagh.

Geologically this area of county Fermanagh falls between the Sligo syncline to the south-west (Oswald 1955), and the Omagh syncline to the north-east (Simpson 1955). While being closely comparable to the Sligo syncline stratigraphically, the area also shows transitional features between these two adjoining regions. In recent years Turner (1951), Padget (1952, 1953), George (1953), Oswald (1955), Simpson (1955), George & Oswald (1957) and Schwarzacher (1961) have described areas surrounding mid-Fermanagh or touched upon its geology in general terms. However, the area has not been described since the mapping of the Geological Survey of Ireland (Symes & Wilkinson 1886). These authors recognized the main elements of the stratigraphy and assigned them to Lower, Middle and Upper groups of the Carboniferous. The argillaceous limestones and shales were termed " calp ", and this name lingers on to the present. The reefal limestones were not differentiated, although it was recognized that the cliffs of Knochmore are " so massive that it is hard to detect bedding ". Within the studied area only one fossiliferous locality (Symes & Wilkinson 1886 : 18, locality 7) was mentioned, and from it only crinoids and _Pentremites_ were listed. The following 15 species of brachiopods were recorded of which only 4* came from localities close to the present area :

*_Athyris ambigua_
Athyris planosulcata
Chonetes hardrensis
Orthis resupinata
Productus giganteus
Productus punctatus
Productus scabriculus
Productus semireticulatus
Rhynchonella pleurodon
*_Spirifera bisulcata_
*_Spirifera glabra_
Spirifera striata
Spiriferina cristata
Streptorhynchus crenistria
*_Terebratula hastata_

A further 7 species from the Carboniferous rocks of Sligo and Leitrim were reported by Symes & Wilkinson (1885 : 33):

Chonetes papilionacea
Orthis michelini
Productus aculeatus
Productus fimbriatus
Productus margaritacea
Spirifera laminosa
Spirifera pinguis

The 7 productoid species listed above, and collected from a wide area, compare with the 16 species of this group recovered from beds at about the same stratigraphic level at Bunnahone and Carrick Loughs.

The local stratigraphy consists of a predominantly argillaceous and calcareous series, referable to the uppermost Benbulben Shale and the Glencar Limestone of Oswald (1955), which occurs below the Dartry group. These boundaries are gradational and poorly fixed, as is that between the Glencar Limestone and the non-reefal Dartry Limestone. The reef limestones are based upon the Glencar rocks but are developed principally within the overlying Dartry group. It is from a single limestone bed towards the top of the Glencar series that the bulk of the silicified faunas has been collected. The limestone bed, between 21 and 23 cm. thick, crops out on the south side and across the bed of the Sillees river, about 250 yards downstream from the old exit of Bunnahone Lough (Text-fig. 2). During the winter of 1962–63

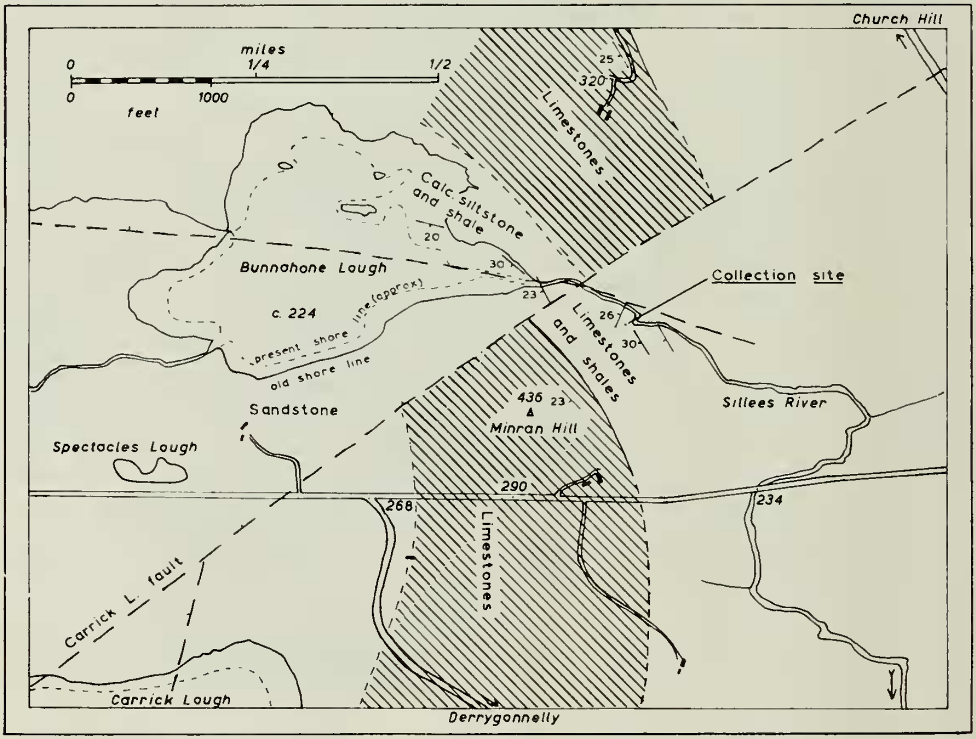

FIG. 2. Map of the Bunnahone region showing the site by the Sillees river from which the silicified faunas were collected. Minran hill is the most northerly of the exposed reef-knolls in the Dartry Limestone (shaded) of this region in Co. Fermanagh. Reefal limestones are again exposed on the south shore of Carrick Lough and subsiduary collections were made there. The shore-lines of both loughs are as on the 6-inch Ordnance Survey maps, but dredging has lowered the water levels so that their shores have receded to approximately that shown by the dashed lines.

Faults in bold dashed lines ; heights in feet.

the level of the Lough water was lowered by about 3 feet so that in normal climatic conditions the length of the river is now extended, for approximately 75 yards westwards over the old Lough floor. The lower one-third of the limestone bed is muddy, containing "pebbles" comparable to the "limestone conglomerate" of Schwarzacher (1961 : 1495). Above this the bed becomes a clean biomicrite and yields a rich fauna. The top few cm. are again muddy and sparsely fossiliferous.

The reefal and non-reefal facies of the Dartry group are strongly contrasting. The reefal areas of Carrick, Knockmore and Killydrum are similar to those of north-east England described by several authors, including Bond (1949, 1950) and Black (1950, 1953, 1954). These rocks contain a brachiopod fauna that differs from those collected from the underlying limestones. The whole of the Dartry exposure, in this region of Fermanagh, becomes regularly bedded and commonly slightly chert-bearing before the deposition of the shales and sandstones at the top of the local succession.

Limestone blocks with a volume of up to 15,000 cubic cm., collected from the Bunnahone area, were etched in dilute hydrochloric acid. Acetic acid was found to be much slower in action and failed to yield additional material. All the etch residues were scrutinized, in water, under a binocular microscope to avoid the loss of minute specimens. The labour of this has been rewarded by the collection of juvenile valves of several species which show structures hitherto unrecorded.

Statistical methods have been applied whenever the size of the sample was sufficiently large and well preserved to allow for quantitative studies in variation. Williams (1962) has discussed the use of statistics as a tool in the taxonomic study of brachiopods and some of the procedures advocated by him have been followed. Paired measurements of skeletal attributes have been converted into estimates of growth and variability by the use of bivariate analysis techniques of Kermack & Haldane (1950). The statistical tables presented here give the mean of each attribute and its variance; "r", the coefficient of correlation between the attributes, and "a", the growth ratio between the variable attributes, together with its variance. Where allometry affected the sample the data is presented in the form Log_e. In comparisons of external ribbing Williams (1962) use of the nouns costae and costellae have been used, viz. costa = a primary rib, "originating at the protegulal node ; and costella = a secondary rib, one which arises by branching or intercalation anterior to the umbonal zone".

I wish to thank Professor A. Williams for all his assistance during my study of the Fermanagh brachiopods while working in his department at Queen's University, Belfast, and for reading the manuscript. I am grateful to Dr. H. M. Muir-Wood of the British Museum (Natural History), Professor J. Mitchell of Galway University College, and Dr. G. A. Cooper of the United States National Museum for their co-operation in lending specimens in their care ; to them, and to all those who have assisted in numerous ways I extend my thanks.

III. PRODUCTOID MORPHOLOGY

The Strophalosiacea and Productacea here described form part of a rich and well preserved brachiopod fauna. The fine silicification of these shells has enabled the study of interiors that were previously poorly known and of juvenile structures hitherto unrecorded. The faunas comprise shells and valves of a wide size range so that ontogenetic variation in features, such as the cardinal process, has been possible.

While it is hoped to deal at greater length elsewhere with these features, a few brief remarks regarding the more important points that have emerged from this study should be mentioned. Perhaps the most important contribution to our knowledge of brachiopod faunas is that gained from the well preserved juvenile valves. Small spines that curl in a clasping fashion around the ventral umbo of productaceans have been recognized for a long time, but it now seems clear that all the genera here described were furnished with such spines. Their development was most probably genetically controlled, but their growth was capable of alteration in response to foreign objects. Moreover, it has now been demonstrated that at least some juvenile species of *Productina, Krotovia, Plicatifera, Eomarginifera* and *Avonia* possessed a pedicle sheath (Brunton 1965) and this is mentioned under the species concerned and figured in the present work (Pl. 7, figs. 1, 4, 5). Until now the supposed absence of a

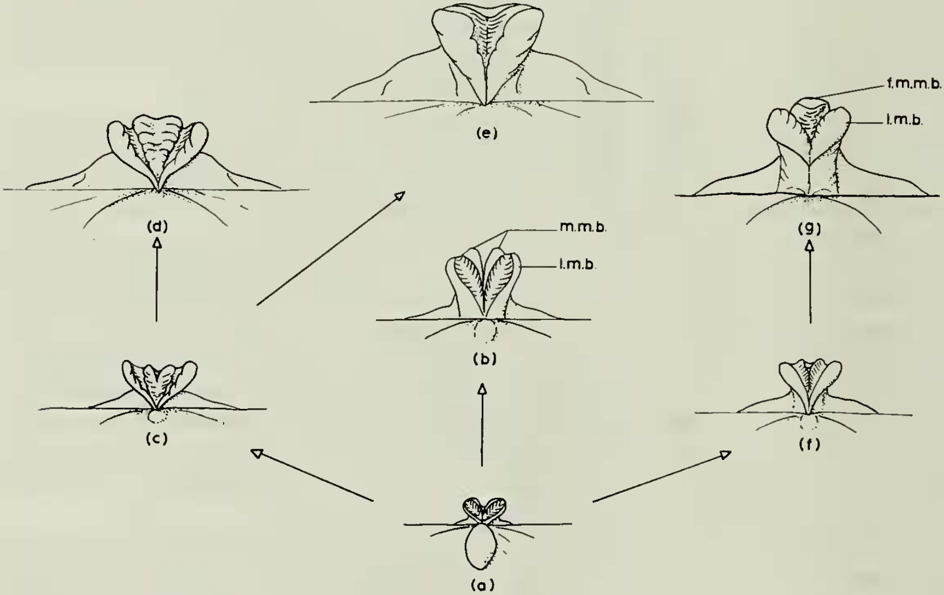

FIG. 3. Stylized illustrations of four principal ontogenetic trends in the development of the productoid cardinal process. (a) : generalized juvenile stage with the two myophore lobes well separated. The diductor muscle bases, accommodated on each lobe, are enclosed by shelly muscle boundaries ; *l.m.b* : lateral muscle boundary ; *m.m.b.* : median muscle boundary. (b) : adult quadrifid cardinal process ; (c) and (d) : the development of the trifid cardinal process by the fusion of the median muscle boundaries over which the diductor muscle bases spread ; (e) : excessive growth of the lateral muscle boundaries which surround the diductor muscle bases ; (f) and (g) : the development of the trifid cardinal process with a shaft by the antero-median fusion of the lateral muscle boundaries. *f.m.m.b* : fused median muscle boundaries.

pedicle sheath was taken as strong evidence for the separation of the productoids from the chonetoids and other strophomenoid stocks known to possess such a structure. It would now seem more natural to reunite these two spinose groups of the strophomenoids at subordinal level.

The presence of a pedicle sheath and juvenile clasping spines indicate that after the free larval stage, these animals were fixed in their earliest stages of development. However, many genera became more or less free-living later in life.

Ontogenetic changes to the cardinal process of most species follow distinctive patterns, but are such as to have altered its appearance considerably at different developmental stages (Text-fig. 3). Fagerstrom & Boellstorff (1964) have illustrated the changes that occurred during the ontogeny of the cardinal process of *Juresania nebrascensis* and pointed out the need for care in its use taxonomically. In the past inordinate emphasis has been placed on the cardinal process as a taxonomic criterion as a result of which inflexible nomenclature has arisen describing its various forms. A study of the cardinal process in a wide range of productoids in all growth stages shows that they are all based upon a bilobed form. The paired diductor muscle bases were attached to these two myophore lobes. The various so-called " trilobed " and " quadrilobed " processes developed as a result of a varying degree of median fusion of the basic two lobes. It is suggested, therefore, that " lobe " should be restricted to the basic structure to which muscles were attached and that the appropriate prefix with the root " fid " be employed for later developmental stages of the cardinal process. In this way the cardinal process in which the two myophore lobes had completely fused medianly should be called trifid (Text-fig. 3, d); that in which the lobes were deeply incised, but not medianly fused, should be quadrifid (Text-fig. 3, b).

Brachial impressions and the possible traces of a mantle canal system are described under the genera in which they have been observed most clearly, e.g. *Overtonia* and *Eomarginifera*.

A stylized productacean ontogeny

All extinct brachiopods probably spent a time as free planktonic larvae during which their numbers were vastly reduced by predation and other factors of a competitive environment. Some environmental or physiological stimuli induced settlement of the surviving spat on to the sea-floor, during which many more individuals were lost. It is possible, however, that the larvae had a small degree of selective power enabling them to better their chances of survival at this stage. It is believed, that in common with most strophomenoids, the productacean spat were provided with a posteriorly developed thread-like pedicle, surrounded by a short skeletal sheath, which was used to make the primary attachment to some solid object, such as skeletal debris, living material, or even large sand grains. The larval form is represented by the protegulal nodes of each valve, commonly 0·2 to 0·3 mm. long, and in some genera distinctly bipartite on the pedicle valve. The rudimentary brephic valves soon developed and the ventral one commonly had a distinct groove along its length which was about 0·2 mm. wide (Text-fig. 4, a, d). This may have been an impression left by the primary anchoring object, but it is not always so, and it seems more likely that it resulted from a differential growth rate within the ventral valve, which perhaps reflects a juvenile development of the muscles. The first pair of spines encircled this groove, at about one-half the brephic valve length, viz. about 0·5 mm. from the beak, and were sometimes so placed as to have grown around some slender object, like a bryozoan stalk. The regularity of spine development indicates that it was genetically rather than phenotypically controlled. Two or three additional pairs of clasping spines developed close to the hinge-line, up to a distance of about 2·0 mm. apart, on the young neanic pedicle valves about 1·5 to 2 mm. long. These spines grew postero-ventrally and arched the pedicle umbo so that they occasionally encircled a piece of shelly debris (Pl. 7, figs. 1–3), commonly that to which the spat first attached itself. By this stage, 1·5 to 2 mm. long, the adult ornament of the valve was beginning to develop. As well as growth-lines, rugae and/or costae were distinguishable. Grant (1963 : 134) reports the occurrence in *Linoproductus* of clasping hinge spines having continued to form along the full width of the hinge-line throughout life, but this appears to be unusual amongst Productaceae as a whole. Up to a length of a few mm. the young shell was probably firmly anchored ; during the brephic stage by the pedicle, and later by the small spines clustered around the umbo. Later it is probable that most shells lost their

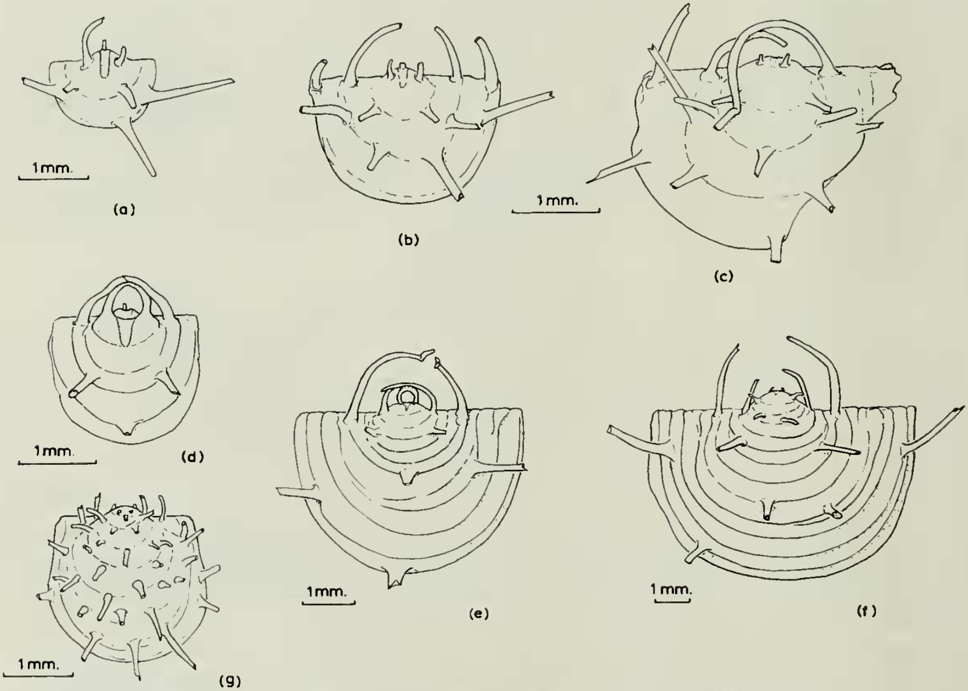

FIG. 4. Illustrations of juvenile pedicle valves : (a–c) *E.* (*Eomarginiferina*) *trispina* subgen. et sp. n. ; (d–f) *Plicatifera plicatilis* (J. de C. Sowerby) and (g) *Krotovia spinulosa* (J. Sowerby), showing patterns of spine arrangements, the posterior clasping spines, and the postero-median pedicle sheath.

firm attachment and became more or less free-living on the sea floor. There are, however, many exceptions to this, such as the scachinellids and richthofenids and those abundantly spinose genera like *Spinulicosta*, which must have grown together in crowded colonies with their spines entangling with one another ; moreover, many strophalosids remained cemented to some solid object by their pedicle valves.

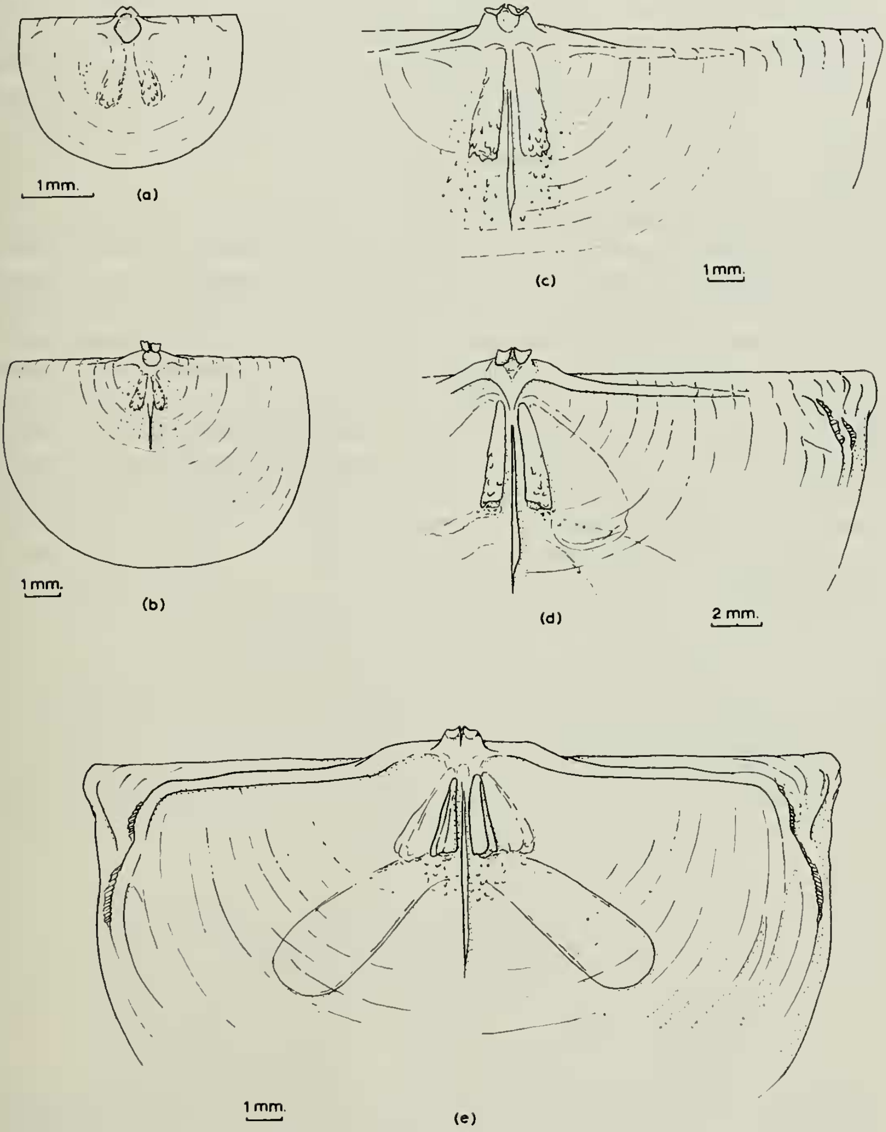

Fig. 5. Stylized illustrations, based upon *Plicatifera plicatilis* (J. de C. Sowerby), of the ontogenetic development of the productacean brachial valve interior.

Within the Fermanagh shells the cardinal process is distinguishable in the smallest available valves, 1·2 mm. long, and by about 2 mm. long the rudiments of the lateral ridges had developed (Text-fig. 5, a). The adductor scars formed next and in valves 5 mm. long the median septum was commonly distinguishable between and anterior to the adductor scars (Text-fig. 5, b). In the pedicle valve the adductor scars were commonly differentiated before the diductor scars. The small umbonal spines were sealed by secondary shell at various stages of development, leaving only the marginal spines in a living condition. The growth of the brachial valve kept pace with that of the pedicle valve and anteriorly the two curved together, but a trail was not formed until after the development of the visceral disc. Thus the onset of the trail occurred at very varied shell lengths in different genera.

Most of the Productacea have strongly curved pedicle valves and less curved brachial valves. This was achieved by the slower growth-rate of the brachial valves, which in consequence usually have a more crowded concentric ornament, e.g. rugae, lamellae or spines (Text-fig. 6). This curvature also meant that up to maturity, when the visceral disc was fully developed, the brachial valve rotated about an axis at the hinge-line. This would have led to the formation of a continued gap, or a poor fit of the posterior margin had it not been for the development of the posteriorly placed lateral ridges which extended laterally throughout growth (Text-fig. 5, c–e). Towards adulthood lateral growth close to the hinge-line accelerated in some groups and led to the formation of ears. After maturity, while a slow dorso-anterior growth continued, lateral growth commonly ceased, so that the shell gradually became more curved in profile.

If rugae had developed across the visceral region, they stopped at this stage although radial ribbing continued to the anterior margin. The brachial valve

(a)	Overtonia fimbriata					
rugae	1–4	5	6	7	8	9
brachial valve	2·7	3·6	4·5	5·3	6·3	7·5
pedicle valve	3·3	4·8	6·6	8·8	11·6	12·6

(b)	Avonia (Quasiavonia) aculeata		
brachial valve	4·5	6·0	7·0
pedicle valve	6·0	8·0	10·8

FIG. 6. Measurements along the valve surface from the umbones to the rugae of *Overtonia fimbriata* (J. de C. Sowerby), (a); and various lamellae on *Avonia* (*Quasiavonia*) *aculeata* (J. Sowerby), (b), that can be identified on both valves in order to compare the relative lengths of pedicle valves and their matching brachial valves.

curved strongly, or geniculated against the pedicle valve to form a common antero-dorsally directed trail.

Internally, the cardinal process developed progressively from its early distinctly bilobed condition (Text-fig. 3). The same basic bilobed pattern can be traced through all the modifications leading to the typical adult cardinal process because of the constraint exercised by the paired muscle bases. Commonly, the cardinal process grew posteriorly, the myophores facing postero-dorsally, and as development proceeded the two lobes became increasingly fused anteriorly by the deposition of secondary shell. At the same time the outer ridges of each myophore curved around the muscle bases to a greater or lesser extent. In this way the outer face of the cardinal process became " folded " to the quadrifid condition, when not medianly fused, or trifid when the two median muscle boundaries had completely fused (Text-fig. 3, d). Further posterior growth and migration of the muscle bases towards the tip of the cardinal process left the base free for the deposition of secondary shell and the formation of a shaft separating the myophores from the base (Text-fig. 3, g). In groups with strongly demarcated ears, ridges developed across their inner margins quite early in life and, with the thickening of the dorsal valve at maturity, commonly fused to the lateral ridges. These ridges continued around the lateral and anterior margins of the visceral disc in some marginiferids.

Brachial ridges became prominent after the development of the visceral region. The outer mantle epithelium deposited secondary shell over the surfaces to which nothing was strongly attached so that the anterior adductor scars usually became strongly outlined while the posterior scars became distinguishable. The median septum was thickened and a ridge commonly developed connecting it to the base of the cardinal process, in so doing usually filling the protegulal cavity, or alveolus (Text-fig. 5, a). The " drag " of the suspended lophophore probably folded the mantle and this led to the development of the strong brachial ridges and the thickenings within the brachial areas of some genera. The pinnate mantle canal system, possibly leaving its trace on the shell in the form of radial ornament, spread anteriorly between the rows of more or less radially arranged tubercles, or between the stronger ridges developed ventrally in some genera, viz. *Eomarginifera* (Pl. 16, fig. 19). Although the radial ornament was developed from the early neanic stages, it became accentuated during growth and this may have been because of the increased development of the mantle canal system. Within genera such as *Avonia* the late development of a radial ornament may be associated with the maturity of gonadal tissue in the mantle canal system. The ridges that developed across the floor of the pedicle valves of certain marginiferids, buxtoniids and dictyoclostids were probably deposited between a pinnate mantle canal system, comparable to that of *Leptagonia analoga*.

Spines are one of the most striking features of the productoids, which together with the chonetoids are the only spinose Strophomenida. Spines are varied in form and probably in function, but developed in similar ways. Where ribbing is present the spines are located close to their crests. It is believed that ribbing in the productoids is commonly associated with the mantle canals and setal follicles at the mantle edge. Spine development probably started at the mantle edge as generative buds of outer epithelium containing a strand of the mantle canal system which supplied nutrients to the growing tip. Thus, ribbing, spines and mantle canals are probably all associated. It has been recognized for a long time that spines must have contained living tissue, but it was Williams (1956 : 252) who gave the most realistic picture of their growth as " disjunct portions of the tip of the outer epithelium, occupying the ends of the spines and capable of proliferation of secretory cuboidal epithelium independent of the mantle edge ". This concept allows the spine to have grown continually, while the epithelium remained active, and permitted its growth to alter in response to contact with solid objects. This occurred (Pl. 5, figs. 4, 14, 15) by envisaging the shell secretion to have taken place just behind the generative tip of the spine.

By adulthood most spines, except those at the shell margins, had been blocked by shell deposition internally, and had died. However, during growth the spines must have grown rapidly while still close to the valve margins.

In genera such as *Eomarginifera*, with a few major spines that developed only at the onset of adulthood, the spines commonly retain internal connections despite being left well back from the valve margin. These long straight spines most likely acted as stabilizers to the shell after the rotation of the body cavity, relative to the substratum, had ceased.

Throughout adult life some secondary shell deposition took place which accentuated the internal morphology and which possibly continued to modify the cardinal process. Once migration of the muscle bases had ceased, as probably happened after maturity, the muscle scars underwent little change, other than accentuation of outline. The principal anterior and marginal spines retained internal connection and continued to act as stabilizers to the shell until its death. Their internal openings became rimmed and the tubercles increasingly thickened or buried by secondary shell. Extensions and retractions of the anterior mantle margins commonly led to the formation of lamellose frills and thickenings along the margins of the shell.

Eventual death of the brachiopod led to the loss of any active attachment to the substratum, so that the shell became free to be acted upon by sea currents and commonly became a suitable habitat for many epifaunal invertebrates.

IV. SYSTEMATIC DESCRIPTIONS

Superfamily **STROPHALOSIACEA** Schuchert 1913

Family **STROPHALOSIIDAE** Schuchert 1913

Subfamily **STROPHALOSIINAE** Schuchert 1913

EMENDED DIAGNOSIS. Strophalosiidae with no spines on brachial valve.

Genus ***STROPHALOSIA*** King

1844 *Strophalosia* King : 313.
1846 *Strophalasia* King : 28, 92.
1850 *Strophalosia* King : 93 (pars).

EMENDED DIAGNOSIS. Outline subcircular to transversely elliptical with straight hinge-line about two-thirds maximum width, ventral umbo developed but commonly deformed by cicatrix of attachment ; profile gently concavo-convex, adult brachial valve forming short trail ; ornament of variably developed lamellae, commonly more prominent on brachial valve, spines restricted to pedicle valve, differentiated into prostrate and more or less erect series ; brachial valve spine-free but dimpled ; ventral interarea anacline to orthocline, extending full hinge width, delthyrium narrow, triangular, closed by slightly arched pseudodeltidium ; dorsal interarea hypercline, shorter and with narrow indistinct chilidium ; teeth rounded in outline and oblique to valve margin ; cardinal process elongately narrow, quadrifid to trifid but thickened in old-age, supported by posteriorly low median septum and curved socket ridges, indistinct in adulthood ; adductor scars slightly raised, smooth, elongately oval and not clearly divided ; brachial impressions indistinct, lobate ; ventral interior unrecorded.

TYPE SPECIES. *Strophalosia gerardi* King, by subsequent designation of the International Commission on Zoological Nomenclature (1962, Opinion 625).

DISCUSSION. The interpretation of the genus has been controversial from its erection in 1844 owing to the lack of an established type species. In recent years Maxwell (1954), Muir-Wood (1960) and Waterhouse (1964) have discussed the genus and on the application of Muir-Wood the International Commission on Zoological Nomenclature has designated *S. gerardi* King 1846 as type species. While clearly setting out the complex history of the genus, this ruling, unfortunately, includes errors which detract from its validity and *S. gerardi* is so poorly represented in known collections that it remains difficult to give a full description of the genus, based upon the type species.

Within the strophalosiinids considerable weight has been given to the taxonomic importance of the presence or absence of spines on the brachial valve ; species with such spines having been assigned to the Strophalosiinae and those without to the Heteralosiinae.

The two type specimens of *S. gerardi* (Pl. 1, figs. 7–9) collected from the Himalayas and kept at University College, Galway, Ireland, have been studied and no trace of spines can be seen on the brachial valves, neither on the external nor internal surfaces, or within the shell structure. This observation has already been made by several authors (e.g. R. H. King 1938, Waterhouse 1964). The external surface of the brachial valve is somewhat lamellose and ornamented by irregular dimples, similar to those commonly seen on *Heteralosia* R. H. King, but neither spine bases nor spines have been found in the adjacent sediment. *Heteralosia* was separated from *Strophalosia* by R. H. King (1938 : 278) to include species " that have a smooth dorsal valve ", and he assigned *S. gerardi* to his new genus believing that *Orthis excavata* Geinitz was the type species of *Strophalosia*. Thus, although common usage has placed species with spinose brachial valves into *Strophalosia*, the ruling of the International Commission necessitates a revision of the Strophalosiidae, including the placing of *Heteralosia* and *Strophalosia* into the same subfamily. A suitable genus must also be found for the spinose species previously assigned to *Strophalosia*.

A study of topotypic specimens of *Heteralosia slocomi* R. H. King (Pl. 1, figs. 1–4), type species of *Heteralosia*, from the Graham formation near Gunsight, Texas, shows that they are distinct from *S. gerardi*. The Texan shells are about two-thirds the length and width of the Himalayan species and associated with this difference are apparent differences in the spine pattern of the pedicle valves, surface ornamentation and development of the interarea. However, these differences are not so clear in a comparison of the specimens as they would have appeared when both species were of much the same dimensions. For example, the spine bases of both species measure 0·4 mm. in diameter, 10 mm. from the pedicle umbo, and the spine frequency was probably comparable. Unfortunately, it is not possible to compare the internal morphology of the species at similar developmental stages, but the Himalayan brachial interior is comparable to an older developmental stage of the Texan species, assuming normal shell deposition within *H. slocomi*. The stratigraphic position of *S. gerardi* is not known accurately, but is commonly recognized as being Permian. *H. slocomi* comes from the Upper Pennsylvanian of Texas and the genus probably extends into the Permian. The question as to whether *Heteralosia* should be treated as a junior synonym of *Strophalosia* is, therefore, one of opinion regarding size and geographical distribution. The likelihood of obtaining further Himalayan specimens is remote. Congeneric specimens from Tasmania, comparable in all recognizable external features and attributed to " *S. gerardi* " are known from mid-Permian strata. It is to be hoped that more Tasmanian material might assist in the comparison of these genera, but until such a study can be made it is better to retain the two genera, while recognizing their morphological similarities.

One Tasmanian specimen (98216) of " *S. gerardi* " (Pl. 1, figs. 5, 6), in the British Museum (Natural History), has four juvenile shells of from 3·4 to 5·6 mm. wide attached to its pedicle valve. These young shells are transversely elliptical to rectangular in outline and their pedicle valves are in close contact with the adult *Strophalosia*. Spines extend from their pedicle valves, but there is none on the brachial valves.

The brachial valve interior of *S. gerardi*, which accompanies the holotype from the Himalayas, shows a number of informative features. The specimen is partially delaminated and most of the cardinal process has been broken. However, a juvenile stage of development within the cardinal process is exposed, showing it to have been elongately narrow, with slight shoulders on the flanks, anterior to the fused median muscle ridges. This juvenile stage is similar to the cardinal process of *Heteralosia* cf. *fortispinosa* (Pl. 4, fig. 11) from Fermanagh, indicating a point of similarity between these groups. Prominant socket ridges extend at a high angle from the cardinal process base in *S. gerardi*, and these flank the postero-lateral margins of the smooth, slightly raised adductor scars. This contrasts with *Dasyalosia* and *Orthothrix* in which the socket ridges are short, barely reaching the posterior margins of the adductor scars.

More features than that of a spine-free brachial valve link *Strophalosia* and *Heteralosia* and the two genera are here united within the same subfamily, Strophalosiinae Schuchert 1913, which has priority over Heteralosiinae Muir-Wood & Cooper 1960. The strophalosiid genera with spines on both valves (*Crossalosia*, *Dasyalosia*, *Eostrophalosia* and *Orthothrix* of Muir-Wood & Cooper's classification, 1960 : 65) are thus left without a subfamilial status. Of these genera *Dasyalosia* is the best known, and being well represented has been chosen as the type genus of the new subfamily Dasyalosiinae. It may prove necessary to redistribute the genera within these subfamilies, but such a revision is beyond the scope of the present work.

In discussing *Strophalosia*, Muir-Wood (1960 : 316) correctly points out the priority of *Productus spiniferus* Howse and *P. morrisianus* Howse over the respective names *Strophalosia morrisiana* King and *S. spinifera* King. This use of the same specific names by different authors arose because Howse used manuscript names of King that had already been published (*in* Murchison & Verneuil 1845) before King's determinations were made known. Howse's descriptions were published two days before King's and should therefore be accepted. It is unfortunate that Muir-Wood concludes by requesting the suppression of Howse's names in favour of those given by King. (This request was granted by ICZN 1962, opinion 625.) De Koninck (1847 : 263) records his difficulty in comparing his species, *P. lewisianus*, with those of Howse and King because of King's refusal to lend material. It is clear that *S. spinifera* King (= *P. morrisianus* Howse) is synonymous with *P. lewisianus* de Koninck and both came from Humbleton, Durham. *S. morrisiana* King (=*P. spiniferus* Howse) is distinctive in being finely ribbed as well as spinose, but its modern generic position remains to be determined.

Genus ***HETERALOSIA*** R. H. King

Heteralosia cf. ***fortispinosa*** (Hinchey & Ray)

(Pl. 4, figs. 9–19 ; Pl. 5, figs. 1–5)

Description. Outline subrounded, length almost equal to maximum width at midlength of shell ; ventral umbo variable, commonly extending beyond hinge-line which is about three-quarters maximum width, cicatrix of attachment variably developed, ears small, triangular ; profile concavo-convex, depth about two-fifths length ; spines confined to pedicle valve, arranged concentrically and more or less in alternating radial rows of variably disposed erect spines and recumbent spines following shell profile, growth lines on both valves, rarely becoming prominent to lamellose on brachial valve ; ventral interarea apsacline to orthocline with elongate trigonal delthyrium, apically closed by slightly arched pseudodeltidium and filled by dorsal surface of cardinal process ; dorsal interarea much reduced ; teeth small, semi-oval in outline and cross-section, commonly laterally divergent at low angle from hinge-line ; muscle scars poorly defined, apparently lobate and confined posteriorly ; scattered spine openings and row along inside of hinge-line, short sharp tubercles medianly placed ; cardinal process prominent, commonly tapering postero-ventrally, lobes tightly compressed, median myophore ridges narrow on external surface forming bifid distal tip, lateral myophore ridges poorly developed ; socket ridges short, supporting cardinal process, at about 40° to hinge-line but laterally recurring towards it and dying out within about 1 mm.; median septum wide posteriorly at base of cardinal process, extending anteriorly for about one-third adult valve length, becoming narrow and higher ; adductor scars oval, extending about one-half length of septum and variably enclosed postero-laterally by secondary thickening from socket ridges ; radially arranged spinose tubercles medianly ; shell substance pseudopunctate.

MEASUREMENTS (in mm.)	length	width
Complete shell (BB.52813)	5·8	9·6
Complete pedicle valve (BB.52814)	7·5	8·7
Complete pedicle valve (BB.52815)	5·0	5·5
Incomplete pedicle valve (BB.52816)	8·5	—
Incomplete brachial valve (BB.52818)	*c.* 5·5	—
Complete brachial valve (BB.52819)	5·5	6·0
Complete brachial valve (BB.52820)	3·0	3·0
Complete pedicle valve (BB.52821)	2·3	2·3
Complete pedicle valve (BB.52822)	2·0	1·8
Complete pedicle valve (BB.52823)	1·4	1·6
Incomplete pedicle valve (BB.52824)	—	*c.* 6·5
Complete pedicle valve, attached (BB.52825)	5·4	6·0
Complete pedicle valve, attached and distorted (BB.52826)	2·7	2·8

LOCALITIES AND HORIZON. Subreefal limestones and shales, Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. *Heteralosia* was previously unrecorded from the British Isles, except for an unnamed species from the Permian near Ripon, Yorkshire, referred to by Muir-Wood & Cooper (1960 : 81). Otherwise, the species assigned by these authors to *Heteralosia* are all from the Mississippian or Pennsylvanian of the American continent. *Heteralosia fortispinosa* (Hinchey & Ray 1935), as illustrated by Muir-Wood & Cooper (1960, pl. 3, figs. 1–5), agrees in known characteristics with the Fermanagh shells, except that the latter are rather smaller in all proportions than those from America. Thus until type material of *H. fortispinosa* can be studied, the Fermanagh shells are identified as *H.* cf. *fortispinosa*.

The species is not strongly curved and peripheral growth of the shell appears to have been isometric. The maximum width is consistently about 10% greater than length. The ventral umbo gives a somewhat rounded outline to the posterior margin, while the hinge-line of the brachial valve is straight ; the ears are small on both valves. The postero-ventral surface of the ventral umbo is variably deformed by the cicatrix of attachment, which only rarely is not visible. Usually it is about 1 mm. in diameter and many of the posteriorly placed spines may be deformed distally, where they came into contact with some hard object. In a few instances fragments of shelly material are preserved adhering to the cicatrix, and it is possible to observe the deflection of the spines as they grew into contact with this material (Pl. 5, figs. 4, 15). It is common for such spines to become distorted and somewhat swollen, as if to make a firmer attachment, and this habit indicates that the shell substance of the spines must have grown behind a slightly protruding bud of outer epithelium. In itself, this bud, was probably of importance in anchorage, and it did allow the growth of the spines to alter in response to contact. The shells show a genetic characteristic which further aided attachment. The alternate rows of more highly angled spines, which appear to have been added during growth by intercalation between dichotomizing rows of the recumbent spines, always grew in a postero-ventral direction, so that as growth continued the more anteriorly placed spines grew back along the shell in an opposite direction to, and only at a slightly higher angle than, the anteriorly directed recumbent spines (Pl. 5, figs. 9, 13). In other words, the constancy of growth direction led to a considerable and progressive alteration in the angle of the spines to the shell surface, and resulted in the maximum contact of spines with the posteriorly placed object of attachment. It is common for the silicified material to have lost most of the more erect, postero-ventrally directed spines, but when they are preserved little of the shell surface can be seen through the dense mat of opposed spines.

The ornament of the brachial valve is irregular, consisting of variably developed, rather dimpled, low rugae, showing a tendency to become anteriorly lamellose. This ornament is most clearly defined at the hinge-line. The dimples probably developed at the valve margin, opposite the spine bases on the pedicle valve, when the valves were in close contact and are uncommon on species with lamellose or spinose brachial valves.

The first formed brachial valve, up to 1 mm. in length, was flat but during subsequent growth the valve became evenly concave, although the degree of curvature was somewhat variable within the species. Internally the median septum is just visible as a thickening at the base of the cardinal process in valves about 2 mm. long, but became clearly differentiated in valves 3 mm. long and extended for one-third of the valve length (Pl. 4, fig. 10). The adult median septum remains low over the posterior one-third of this length, but is narrow and high anteriorly.

The adductor scars are usually visible in valves 3 mm. long, but are not distinct until surrounded by secondary shell at a length of between 5 and 6 mm. Variability in the depth and shape of the ventral umbo appears to have led to some variation in the angle of projection of the cardinal process. Most commonly it grew at an angle of about 130° to the commissural plane, but rarely perpendicular. The distal end of the cardinal process is also rather variable ; the two lobes are always narrowly separated by a groove and the median ridges of each myophore are commonly extended posteriorly. The outer ridges of the myophores are rarely developed, but when present arise one-half to two-thirds the way along the dorsal surface of the cardinal process as subsidiary ridges forming shoulders below its tip. The fused basal portion of the myophore produces a low ridge from the dorsal beak which may be the structure called a lophidium by Muir-Wood & Cooper (1960 : 6).

The ventral muscle field is too poorly differentiated to be distinguishable through a growth series. The teeth show no proportional alteration, but in adult valves it is possible to distinguish the overgrowth of the interarea onto their posterior margins, a process which differentiated the teeth more fully from the interarea during growth.

A row of spines close to the ventral hinge-line commonly retained internal connections below the interarea, otherwise the remaining spines only sporadically retained internal openings, and these appear to bear relationship neither with the spines making anchorage to a foreign object, nor to those that grew in a particular direction, i.e. either the erect or recumbent spines.

TABLE 1

$\overline{L}$ mm. (var.) = 4·08 (3·709)
$\overline{W}$ mm. (var.) = 4·30 (4·431)
r = 0·974
a (var.) = 1·093 (0·00175)

$\overline{W}$ mm. (var.) = 4·30 (4·431)
$\overline{HiW}$ mm. (var.) = 2·93 (2·645)
r = 0·965
a (var.) = 0·773 (0·00117)

$\overline{L}$ mm. (var.) = 4·08 (3·709)
$\overline{DelH}$ mm. (var.) = 0·38 (0·040)
r = 0·941
a (var.) = 0·108 (0·000037)

$\overline{DelH}$ mm. (var.) = 0·38 (0·040)
$\overline{DelW}$ mm. (var.) = 0·28 (0·012)
r = 0·836
a (var.) = 0·54 (0·0026)

TABLE 1. Statistics for length (L), maximum width (W), width of hinge-line (HiW), height of delthyrium (DelH), and the width of the delthyrium (DelW) at the hinge-line of 37 pedicle valves of *Heteralosia* cf. *fortispinosa* (Hinchey & Ray).

TABLE 2

$\overline{L}$ mm. (var.) = 3·52 (1·703)
$\overline{W}$ mm. (var.) = 3·94 (2·396)
r = 0·968
a (var.) = 1·186 (0·00638)

$\overline{W}$ mm. (var.) = 3·94 (2·396)
$\overline{HiW}$ mm. (var.) = 3·08 (1·734)
r = 0·969
a (var.) = 0·851 (0·00368)

$\overline{L}$ mm. (var.) = 3·52 (1·703)
$\overline{MsL}$ mm. (var.) = 1·09 (0·346)
r = 0·729
a (var.) = 0·451 (0·00793)

$\overline{L}$ mm. (var.) = 3·52 (1·703)
$\overline{CpL}$ mm. (var.) = 0·36 (0·053)
r = 0·853
a (var.) = 0·170 (0·00070)

TABLE 2. Statistics of length (L), maximum width (W), width of hinge-line (HiW), length of cardinal process, from its base (CpL), and length of the median septum from the same point (MsL) of 14 brachial valves of *Heteralosia* cf. *fortispinosa* (Hinchey & Ray).

Subfamily **DASYALOSIINAE** nov.

DIAGNOSIS. Strophalasiidae with spines on both valves.

Genus ***DASYALOSIA*** Muir-Wood & Cooper 1960 : 76

TYPE SPECIES. *Spondylus goldfussi* Muenster 1839, by original designation of Muir-Wood & Cooper (1960).

Dasyalosia goldfussi (Muenster) was described from the Zechstein of Gara, Germany, and the genus was described by Muir-Wood & Cooper (1960). These authors are incorrect in describing the cardinal process as " not having a lobate myophore ". The dorsal interior figured by them (1960, pl. 6, figs. 16, 17) has a broken cardinal process, as can be seen from conspecific material, also from Gara, in the British Museum (Natural History) (B.73242 and B.73246). From these specimens it is clear that the cardinal process extends well beyond the hinge-line and expands distally so that it can be easily broken close to the hinge-line. The cardinal process of *D. lamnula* (Pl. 3, figs. 8, 9) is closely comparable to that of the German type specimens.

The Fermanagh species not only have similar cardinalia to *D. goldfussi*, but externally they are alike in ornamentation; both have pedicle valves thickly covered by spines that grew in two sets, those growing posteriorly commonly clasping an object such as a productid spine or bryozoan stalk. No clear evidence of actual cementation of the ventral umbo or of a pedicle sheath have been found, but the umbo is commonly flattened against a piece of shell debris. The juvenile clasping spines probably assisted in the fixation of the young shells. The spine pattern of *D. goldfussi* is similar to that of *D. panicula*, with its preponderance of erect, posteriorly curving spines. They are also similar in having ventral interareas that extend the full widths of their hinge-lines and their brachial valves are more lamellose than their pedicle valves. It is likely that the Carboniferous species was ancestral to the Permian German species.

Both the Irish species are more lamellose than *D. goldfussi*; their erect spines apparently never extended posteriorly to quite the same extent and the valves did not reach the same size as specimens from Germany. The concavity of brachial valves of *Dasyalosia* results from its geniculation against the pedicle valve margin in adulthood, when an increase in the thickness of the body-cavity ceased. Young valves are more plano-convex in profile and the visceral disc is but slightly curved.

At present, only the type species and those species here described from Co. Fermanagh are assigned to the genus.

Dasyalosia panicula sp. n.

(Pl. 2, figs. 1–17; Pl. 3, figs. 1–5)

DIAGNOSIS. Outline subrounded to rounded trigonal, length about equal to maximum width, hinge-line straight, nearly one-half maximum width; umbo pointed, extending beyond hinge-line, rarely with cicatrix of attachment or distorted; profile plano-convex to slightly concavo-convex, about one-third as thick as long; concentric ornament of sublamellose ridges from which arise spines of two series in radially arranged rows; primary and intercalated rows of anteriorly directed recumbent spines alternate with dichotomizing rows of postero-ventrally directed spines which are commonly grouped into threes and widen distally; brachial valve similar, but erect spines not grouped; ventral interarea prominent, concave and orthocline, extending full width of hinge-line; delthyrium narrow, triangular, covered by flat pseudodeltidium; dorsal interarea reduced, about one-quarter length of ventral interarea; teeth prominent, semioval in outline, concave dorsally and commonly diverging at about 25° from hinge-line; adductor scars prominent, upon elongately trigonal platforms separated by median groove, extending about one-third valve length ; diductor scars indistinct, rounded and flanking ; fine spine-like tubercles developed medianly ; spines retain internal openings marginally ; cardinal process laterally compressed, elongate and extending postero-ventrally, median myophore ridges extended and narrowly separated ; commonly broad groove on internal face of cardinal process, laterally enclosed by median ends of supporting socket ridges at about 35° from hinge-line ; sockets deep, externally enclosed by interarea ; adductor scars subrounded to elongately oval, raised and extended anteriorly as tuberculate ridges ; adult median septum about three-fifths valve length, low and broad posteriorly, becoming narrow and prominent anteriorly ; slight lateral ridges across inside of much reduced ears ; spine openings marginal ; tubercles medianly and anteriorly placed, shell substance pseudopunctate.

Measurements (in mm.)		length	width
Holotype.	Complete shell (BB.52790)	10·3	10·5
Paratypes.	Pedicle valve (BB.52791)	*c.* 8·0	8·2
	Incomplete pedicle valve (BB.52792)	*c.* 7·6	7·9
	Complete pedicle valve (BB.52793)	3·1	3·2
	Complete brachial valve (BB.52794)	6·0	6·2
	Complete brachial valve (BB.52795)	3·4	3·9
	Complete shell (BB.52796)	4·1	4·3
	Pedicle valve attached to bryozoan (BB.52797)	4·0	3·5
	Incomplete pedicle valve on bryozoan (BB.52798)	4·5	—
	Pedicle valve showing spine growth-lines (BB.52799)	4·0	4·3
	Pedicle valve (BB.52800)	8·0	*c.* 8·4
	Complete pedicle valve on bryozoan (BB.52920)	4·0	4·3

Localities and horizon. Subreefal limestones and shales at Carrick Lough, and sporadically at Bunnahone, about 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

Dasyalosia lamnula sp. n.

(Pl. 3, figs. 6–18 ; Pl. 4, figs. 1–8 ; Text-fig. 7)

Diagnosis. Outline subcircular, length approximately equal to maximum width occurring at mid-length ; hinge-line straight, about two-thirds maximum width ; profile plano-convex to slightly concavo-convex, ventral umbo commonly rounded and extending slightly beyond hinge-line ; about one-third as thick as long ; ventral beak rarely with cicatrix of attachment, rarely distorted ; concentric ornament of prominent lamellose ridges on both valves ; spines coarse, about 0·2 mm. in diameter on ventral valve, arranged in two series of alternating radial rows arising from concentric ridges, one set about normal to shell with rows added by intercalation, other set anteriorly directed, nearly parallel to shell surface, and branching dichotomously ; brachial valve with finer anteriorly directed spines increasing in number anteriorly, and few at high angle and incurving on cardinal extremities ; ventral interarea variably developed, short and confined umbonally, orthocline ; pseudodeltidium flat, partially filling narrow triangular delthyrium ; dorsal interarea much reduced or lacking ; teeth semioval in outline, about as wide as long, diverge from interarea and more or less curved ; adductor scars elongately oval to trigonal, on raised elongate rectangular platform, three-fifths as wide as long and one-quarter valve length, with shallow median groove ; diductor scars indistinct, spreading antero-laterally from adductor scars ; internal spine openings few ; cardinal process bilobed, posteriorly elongate and medianly fused except at distal tip ; myophores postero-dorsally directed, deeply grooved and extending towards dorsal base of cardinal process ; groove between fused lobes extends to ventral base ; short socket ridges at about 50° to mid-line anteriorly enclose short deep sockets, closely flanking cardinal process ; adult valves with ridges at low angle to hinge-line around inside of small ears to antero-lateral margin ; adult median septum one-half to two-thirds valve length, low and supporting cardinal process posteriorly, high and narrow anteriorly ; adductor scars raised, rounded to trigonal, about one-fifth valve length ; shell substance pseudopunctate.

		length	width (mm.)
HOLOTYPE.	Complete shell (BB.52801)	6·5	6·9
PARATYPES.	Incomplete pedicle valve (BB.52802)	c. 15·0	17·0
	Complete pedicle valve (BB.52803)	8·5	10·0
	Incomplete pedicle valve (BB.52804)	4·5	c. 4·0
	Incomplete pedicle valve (BB.52805)	4·4	—
	Complete brachial valve (BB.52806)	9·0	10·5
	Complete brachial valve (BB.52807)	3·6	4·3
	Complete brachial valve (BB.52808)	2·2	2·6
	Incomplete brachial valve showing the cardinalia (BB.52809)	—	—
	Incomplete brachial valve (BB.52810)	—	—
	Complete pedicle valve (BB.52811)	2·2	2·1
	Complete pedicle valve (BB.52812)	1·3	1·3

LOCALITIES AND HORIZON. Subreefal limestones and shales, Bunnahone and sparsely at Carrick Lough, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. The Fermanagh species show little alteration in the proportions of outline during growth, the coefficients of correlation for both length and width, and length and thickness are high (Tables 3, 5) indicating a regular marginal accretion to the shell. The persistence of the allometric relationship between paired parameters in *D. lamnula,* is probably a reflection of the greater curvature of its pedicle valve, and contrasts with the apparently isometric growth of *D. panicula.* It may be that larger samples of *D. panicula* would prove to be allometric.

The ventral interarea of *D. lamnula* is narrowly confined to the umbonal region and does not extend beyond a hinge-line width of about 2·0 mm. This gives the umbonal slopes a high angle and led to the formation of flattened ears. The hinge-line width of these shells is about two-thirds of the maximum width, while the adult interarea is only one-fifth, or less, of the maximum width. This is in sharp contrast to the fully developed interarea of *D. panicula,* which extends to the cardinal extremities.

A feature confined to *D. lamnula,* is the rare slight sulcation seen in the antero-median halves of 5 out of 36 pedicle valves.

The ventral elongate and raised adductor scars are developed in shells only 3 mm. long (Pl. 4, fig. 5) and can rarely be distinguished as a pair of oval elevations, just anterior to the socket ridges, in valves only 2 mm. long. Statistical comparisons of the lengths of the adductor scars compared to the full widths of the adductor fields of either valve show that they have low coefficients of correlation, indicating that their growth was not regular within the sample. Because the correlation coefficient

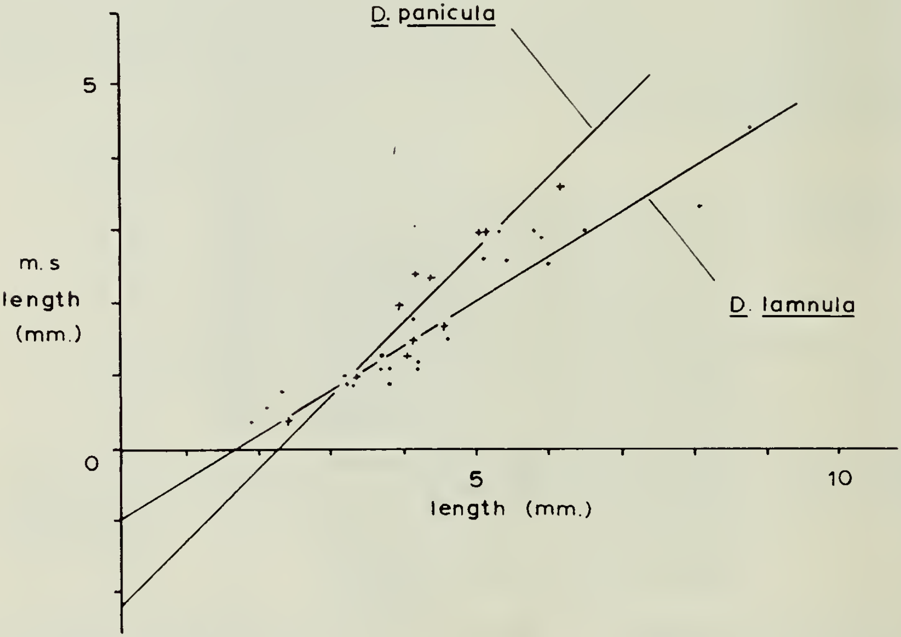

FIG. 7. Plots of the paired measurements of total length of the brachial valve (length) against the length of the median septum (m.s. length) for *Dasyalosia panicula* sp. n. (+), and *D. lamnula* sp. n. (.), illustrating the different growth axes of characteristics for the species.

is not significant ($P > 0{\cdot}01$), the axes of growth for the adductor scars have not been set out in the tables. The dorsal median septum is first seen in shells between 3 and 4 mm. long (Pl. 2, fig. 8). In comparing the brachial valve length with the full length of the median septum, as measured from the hinge-line, a high correlation is obtained. Although the mean length of the median septum is less than half that of the valve, the growth axes, " a", are between 0·62 and 1·00. However, the intersects of these growth axes with the septal length axes are between — 1·0 and — 2·0, so that in both species the start of growth of the median septum might be expected when the valve was about 2 mm. long (Text-fig. 7). The median septum arose between the adductor scars and at the base of the cardinal process and in valves about 6 mm. long grew highest along its anterior margin. In adult shells it was always prominent anteriorly and extended beyond the adductor scars for a little more than one-half the adult valve length (Pl. 4, fig. 2). The median septum appears to differ somewhat in *D. panicula*, in that it grew to about three-fifths of the valve length and arose about 1·5 mm. in front of the cardinal process at a valve length of about 4 mm. Brachial ridges are not distinguishable in either species.

Spines are abundant on each valve of the two species, and arose from the posterior part of each concentric lamellose ridge (Pl. 3, fig. 15). This fixed their position at certain growth stages and they are further located by being radially arranged, a feature seen more readily on pedicle valves than brachial valves because of the alternation, on the former, of erect spines with low angled, or recumbent spines. The spines clearly reached considerable lengths ; a young pedicle valve 2 mm. long has spines of the same length still preserved, while adult shells have broken spines up to 5 mm. long. The differentiation into two sets of spines is primary, being recognized on valves of less than 1·5 mm. long (Pl. 4, figs. 3, 4). Both sets are initially of the same diameter at any growth stage. The erect spines are first anteriorly directed but then curve normal to the shell surface or are postero-ventrally directed. Around the umbo these spines are medianly incurved in a clasping fashion. The alternating recumbent spines arose initially like the erect ones but immediately bent anteriorly to lie more or less parallel to the valve surface and with growth overlap and the more anteriorly placed spines of their row (Pl. 2, fig. 17). A lateral increase in the number of rows of spines was achieved by a diagnostically important pattern of branching and intercalation. In *D. lamnula*, the erect spines form primary and intercalated rows between the recumbent spine rows which bifurcated at each additional intercalation, these occurred at approximately the same growth stage for any one specimen. This contrasts with *D. panicula* in which the arrangement of spines is of primary and intercalated rows of recumbent spines between bifurcating rows of erect spines. Moreover, beyond a pedicle valve length of about 2 mm. the radial rows of erect spines sporadically divided giving groups of three or five spines as prominent tufts, a feature recorded in the specific name. These spines are commonly expanded towards their distal ends and are occasionally somewhat laterally flattened, as if in response to contact with a hard surface (Pl. 2, fig. 9). Such a grouping of three or more erect spines commonly occurred prior to the division of the row as a whole, with the anterior intercalation of a row of recumbent spines. There is a tendency for these erect spines to recurve posteriorly rather more than is usual in *D. lamnula*. The distal ends of the erect spines of *D. lamnula* are never splayed or sharply bent, and thus probably did not come into contact with any solid foreign body, as did those of *D. panicula*. The external ornamentation of the brachial valve of the two species is similar, both having anteriorly directed spines at a low angle to the valve surface, which are of a narrower diameter than those of the pedicle valves. However, erect spines are scattered rather sporadically over the surfaces and concentrated upon the cardinal extremities, especially on the better developed " ears " of *D. lamnula*, where they curve antero-medianly to overhang much of the valve. The dorsal erect spines of *D. panicula* are perhaps more numerous antero-medianly, tend to curve posteriorly and are expanded in a similar way to those of the pedicle valve. Fine growth lines can be seen on the valves and encircling the spines. The most distinctive features which differentiate *D. lamnula* from *D. panicula*, are their spine arrangements, the widths of their ventral interareas and hinge-lines compared to their maximum widths, and the difference of concentric ornamentation. Less distinct differences occur in their dorsal median septa, adductor scars, sulcation of the pedicle valve and deformation of the ventral umbones.

The concentric ridges, from which the spines arose, have prominent lamellose extensions in *D. lamnula*, whilst remaining only incipiently lamellose in *D. panicula*.

Unlike *D. lamnula*, the ventral umbo of *D. panicula* is commonly flattened or distorted by a cicatrix of attachment, or by the presence of some skeletal debris. Several specimens have fragments of bryozoan colonies adhering to their umbones and the posterior erect spines can be seen to cling around these fenistellid stems (Pl. 3, figs. 1–5). Spines curve and cling to such material from a distance of 1·5 mm. Rarely the posterior part of a pedicle valve is dented as a result of its growth around some foreign object and the surrounding spines can be seen to have grown over this material.

Although the slope of the growth axis " a " for length and width, shows no significant difference ($P > 0{\cdot}05$) between the species, *D. lamnula* does seem to have grown larger than *D. panicula* (i.e. *D. lamnula* commonly attained a length of about 15 mm., while *D. panicula* is seldom seen longer than 10 mm. Tables 3 and 5 suggest the converse because of the tendency for large specimens of *D. lamnula* to have been broken). The two are significantly different ($P < 0{\cdot}05$) in regard to their widths of hinge-line compared with their maximum widths ; *D. panicula* having a significantly narrower hinge width. A further important difference is that the ventral interarea extends for almost the full width of the hinge-line, while being confined to the narrow umbonal region of *D. lamnula*. This persistence of the interarea led to the formation of gentle umbonal slopes so that the ventral umbo and ears are less well defined than in *D. lamnula*.

The adductor scars of both species are similarly placed and have comparable outlines, but those of *D. panicula* appear to be less well differentiated and less raised, while the ventral scars of this species do not show the slight ridges seen extending from the antero-lateral corners of the scars of *D. lamnula*. These ridges may mark the trunks of the *vascula media*. The fine spine-like tubercles in the mid regions of *D. panicula* are not so well developed in *D. lamnula*.

From a careful study of the exteriors of these species one might be tempted to consider the differences great enough to warrant generic recognition. This is particularly so in consideration of the differences in the development of the interareas and the different patterns of spine arrangement. However, the similarities of the interiors are such as to indicate a close relationship and one which, in the writer's opinion, does not allow such a division, although it is clear that the two form distinct species groups.

TABLE 3

$\overline{\mathrm{L}}$ mm. (var.) = 5·49 (4·139)
$\overline{\mathrm{W}}$ mm. (var.) = 5·57 (4·459)
r = 0·941
a (var.) = 1·037 (0·0069)

$\overline{\mathrm{L}}$ mm. (var.) = 5·49 (4·139)
$\overline{\mathrm{Th}}$ mm. (var.) = 1·52 (0·389)
r = 0·952
a (var.) = 0·306 (0·00048)

$\overline{\mathrm{W}}$ mm. (var.) = 5·57 (4·459)
$\overline{\mathrm{HiW}}$ mm. (var.) = 3·04 (1·040)
r = 0·973
a (var.) = 0·483 (0·00065)
r_e = 0·987
α (var.) = 0·891 (0·00111)

TABLE 3. Statistics of length (L), maximum width (W), thickness (Th) and width of the hinge-line (HiW) of 20 pedicle valves of *Dasyalosia panicula* sp. n.

TABLE 4

$\overline{\mathrm{L}}$ mm. (var.) = 4·25 (0·917)
$\overline{\mathrm{W}}$ mm. (var.) = 4·76 (1·098)
r = 0·945
a (var.) = 1·091 (0·01423)

$\overline{\mathrm{L}}$ mm. (var.) = 4·25 (0·917)
$\overline{\mathrm{SpL}}$ mm. (var.) = 2·03 (0·926)
r = 0·750
a (var.) = 1·005 (c·0490)

TABLE 4. Statistics of length (L), maximum width (W) and length of median septum from the hinge-line (SpL) in 11 brachial valves of *Dasyalosia panicula* sp. n.

TABLE 5

$\overline{\mathrm{L}}$ mm. (var.) = 3·96 (3·030)
$\overline{\mathrm{W}}$ mm. (var.) = 4·04 (3·956)
r = 0·987
Log$_e$ $\overline{\mathrm{L}}$ (var. log$_e$ L) = 1·287 (0·1774)
Log$_e$ $\overline{\mathrm{W}}$ (var. log$_e$ W) = 1·2925 (0·2175)
r_e = 0·987
α (var.) = 0·903 (0·00089)

$\overline{\mathrm{L}}$ mm. (var.) = 3·96 (3·030)
$\overline{\mathrm{Th}}$ mm. (var.) = 1·29 (0·511)
r = 0·952
Log$_e$ $\overline{\mathrm{L}}$ (var. log$_e$ L) = 1·287 (0·1774)
Log$_e$ $\overline{\mathrm{Th}}$ (var. log$_e$ Th) = 0·1228 (0·2669)
r_e = 0·959
α (var.) = 1·2267 (0·00524)

TABLE V—*contd.*

$\overline{W}$ mm. (var.) = 4·04 (3·956)
$\overline{HiW}$ mm. (var.) = 2·48 (2·156)
r = 0·933
Log$_e$ $\overline{W}$ (var. log$_e$ W) = 1·2925 (0·1774)
Log$_e$ $\overline{HiW}$
(var. log$_e$ HiW) = 0·7602 (0·2995)
r_e = 0·943
α (var.) = 1·174 (0·00664)

$\overline{L}$ mm. (var.) = 3·96 (3·030)
$\overline{AdL}$ mm. (var.) = 0·996 (0·828)
r = 0·501
Log$_e$ $\overline{L}$ (var. log$_e$ L) = 1·287 (0·1774)
Log$_e$ $\overline{AdL}$
(var. log$_e$ AdL) = 0·2995 (0·6070)
r_e = 0·559
α (var.) = 0·586 (0·01026)

$\overline{AdL}$ mm. (var.) = 0·996 (0·828)
$\overline{AdW}$ mm. (var.) = 0·636 (0·076)
r = 0·419

TABLE 5. Statistics of length (L), maximum width (W), thickness (Th), width of hinge-line (HiW), length of adductor scars (AdL) and width of adductor field (AdW) of 25 pedicle valves of *Dasyalosia lamnula* sp. n.

TABLE 6

$\overline{L}$ mm. (var.) = 4·42 (3·024)
$\overline{W}$ mm. (var.) = 4·91 (4·000)
r = 0·970
a (var.) = 1·1502 (0·00344)

$\overline{L}$ mm. (var.) = 4·42 (3·024)
$\overline{SpL}$ mm. (var.) = 1·78 (1·163)
r = 0·949
a (var.) = 0·620 (0·00173)

$\overline{W}$ mm. (var.) = 4·91 (4.000)
$\overline{HiW}$ mm. (var.) = 3·20 (2·287)
r = 0·956
a (var.) = 0·756 (0·00224)

$\overline{W}$ mm. (var.) = 4·91 (4·000)
$\overline{AdW}$ mm. (var.) = 0·51 (0·054)
r = 0·907
a (var.) = 0·116 (0·00011)

$\overline{AdL}$ mm. (var.) = 0·89 (0·164)
$\overline{AdW}$ mm. (var.) = 0·51 (0·054)
r = 0·459

TABLE 6. Statistics of length (L), maximum width (W), width of hinge-line (HiW), length of median septum from the hinge-line (SpL), and length (AdL) and widths (AdW) of the adductor field in 24 brachial valves of *Dasyalosia lamnula* sp. n.

Family **LEIOPRODUCTIDAE** Muir-Wood & Cooper 1960

Subfamily **LEIOPRODUCTINAE** Muir-Wood & Cooper 1960

Genus ***ACANTHOPLECTA*** Muir-Wood & Cooper 1960

EMENDED DIAGNOSIS. Outline subquadrate, hinge-line straight, commonly widest part of shell, umbo rounded extending slightly beyond hinge-line ; profile deeply concavo-convex, not geniculate, body cavity moderately deep ; ventro-anterior fold in slight median sulcus of pedicle valve corresponding to sulcation of brachial valve ; anteriorly directed furrow at valve margin ; radial ornament lacking, concentric rugae poorly defined, low rounded and irregular across about one-half of pedicle valve and brachial valve visceral disc ; growth-lines distinct ; spines commonly confined to pedicle valve, in double row close to hinge-line, sparsely scattered with rough quincuncial arrangement on rugae and over smooth venter, and with low plications extending anteriorly from their bases ; ventral adductor scars poorly differentiated from flanking diductor scars, separated medianly by low median ridge, muscle field finely ridged longitudinally ; hinge-line thickened by angular ridge ; dorsal valve with low broad cardinal process, two lobes fused and raised medianly ; lateral ridges strong, continuing along hinge-line to postero-lateral margins ; adductor scars raised, divisible into elongately trigonal anterior and narrower posterior scars ; median septum low posteriorly, high and blade-like anteriorly ; brachial impressions obscure, elongately lobate, at high angle to mid-line.

TYPE SPECIES. *Producta mesoloba* Phillips 1836, by original designation of Muir-Wood & Cooper (1960 : 170).

DISCUSSION. Emendation of the original diagnosis of Muir-Wood & Cooper (1960 : 170) mainly concerns the brachial valve, which appears to have been described from immature specimens, and which, judging by the present material is very rarely, if ever spinose. An examination of specimen B.13000 (Muir-Wood & Cooper 1960 pl. 44, figs. 10–14) failed to show dorsal spines. The dorsal interior is discussed more fully under the discussion of *A. mesoloba* below. Muir-Wood & Cooper (1960 : 171) state that geniculation occurs in both valves. However, their figure (pl. 44, fig. 13) fails to show this, as do those of Davidson (1861, pl. 31, figs. 6, 9) and Thomas (1914, pl. 20, fig. 21), and the present material. The brachial valve is certainly regularly concave until the furrow at its anterior margin is reached. This concavity is more regular than that of *Plicatifera*. The genus is readily distinguished from *Plicatifera* by its more rounded profile, irregular, low rounded rugae, double row of spines close to the hinge-line, its antero-median fold and distinctive interior.

Acanthoplecta mesoloba (Phillips)

(Pls. 5, figs. 16–22 ; Pl. 6, figs. 1–5)

1836 *Producta mesoloba* Phillips : 215, pl. 7, figs. 12, 13.
1914 *Pustula mesoloba* (Phillips) Thomas : 327, pl. 20, figs. 18–21.
1960 *Acanthoplecta mesoloba* (Phillips) Muir-Wood & Cooper : 170, pl. 44, figs. 10–17.

EMENDED DIAGNOSIS. Subquadrate to subrounded, commonly with prominent ears and hinge-line widest part of shell, length about three-fifths width ; evenly but strongly concavo-convex with moderate body cavity and thickness about three-quarters length, umbo low with gentle slopes ; median fold in shallow sulcus and corresponding fold of brachial valve, to anterior margin from about middle of rugate posterior region ; anterior margins of valves folded antero-ventrally forming transverse furrow ; about 18 to 20 low indistinct rugae developed posteriorly on pedicle valves and complete visceral region of brachial valves ; growth lines prominent ; stout spines almost entirely confined to pedicle valve, suberect from rugae and variably placed in rough quincuncial pattern ; anterior spines and those close to hinge-line retain internal openings ; ventral muscle scars poorly differentiated, ribbed, about one-half length of visceral region ; cardinal process broad and sessile, myophores deeply incised, dorso-posteriorly directed with fused median muscle boundaries ; lateral ridges narrowly divergent from hinge-line in young, but strongly developed along hinge-line in adult, medianly form strong posteriorly directed articulatory platforms at sides of cardinal process ; adductor scars raised, about two-fifths length of visceral disc and about five-sixths as wide as long, divisible into anterior and posterior scars ; median septum from between adductor scars to about one-half valve length, narrow and high anteriorly ; brachial impressions poorly defined, posterior margins at about 75° to mid-line, lobate and extending towards lateral margins ; anterior regions and trail tuberculate.

Measurements (in mm.)	length	width
Brachial valve (BB.52829)	9·0	*c.* 13·0
Incomplete brachial valve (BB.52831)	20·0	*c.* 33·0

Discussion. Specimens are not prolific or well preserved in the Fermanagh fauna so that recourse to previous descriptions and illustrations is necessary to supplement the diagnosis given here.

Muir-Wood & Cooper (1960 : 171) assigned only *A. mesoloba* to their genus and their description of the dorsal interior appears to have been based upon a specimen (possibly pl. 44, fig. 17) which does not show fully developed characteristics (cf. Pl. 5, figs. 20, 21). Development of the dorsal interior was such that in young valves, less than 10 mm. long, the cardinal process was still distinctly bilobed, the lateral ridges were only about one-third of the hinge-line width, and diverged from it at about 15°, the adductor scars and median septum were scarcely distinguishable (Pl. 5, fig. 17). During growth the cardinal process became wider and, as the median muscle boundary ridges of each myophore fused together, overhung a distinct alveolus ; the lateral ridges became increasingly thickened medianly and extended towards the cardinal extremities and the median septum developed, mainly anterior to the ill-defined and longitudinally ridged adductor scars. It was only after attaining approximately maximum dimensions, viz. over about 20 mm. long and about 34 mm. wide, that secondary shell was deposited anterior to the cardinal process, so filling the alveolus, that the raised adductor scars developed and became clearly divisible into anterior and posterior scars, and that the lateral ridges had fully thickened along the hinge-line and formed the strong articulatory surfaces on either side of the myophores of the cardinal process (Pl. 6, fig. 2). At this growth stage also, the brachial impressions started to become visible.

Previous authors have been rather vague about the spinose nature of the brachial valve, although Muir-Wood & Cooper (1960 : 171) correctly describe it as having

" few spines ". The presence of scattered dimples between some of the rugae may be confused for spine bases, but two brachial valves in seven incomplete Fermanagh specimens do show the bases of one spine each.

Genus ***PLICATIFERA*** Chao 1927

1927 *Plicatifera* Chao : 25.
1928 *Plicatifera* Chao ; Chao : 61.
1960 *Plicatifera* Chao ; Muir-Wood & Cooper : 201, pl. 50, figs. 13–23.

TYPE SPECIES. *Productus plicatilis* J. de C. Sowerby 1824, by original designation of Chao (1927 : 25).

DISCUSSION. The genus was redefined and its taxonomic position established by Muir-Wood & Cooper (1960 : 201). The diagnosis of these authors differs from the specific diagnosis given here in not mentioning radial ornamentation and by the absence of dorsal spines. The nature of radial ornamentation has been discussed at length by Thomas (1914 : 333) who concluded that its presence was entirely the result of local " decortication " of the shell. The writer's experience is that both pedicle and brachial valves, show a ribbing beyond a length of about 5 mm. and to a point about mid-way between the last ruga and the anterior margin. This is true not only on the Fermanagh shells but on the type specimen figured by Sowerby (1824, pl. 459, fig. 2), B.M.(N.H.) No. 60960. The ribbing is best seen where it crosses the anterior rugae, but also in the interrugal spaces, where it forms an indistinct reticulation, and immediately anterior of the rugae, close to the point of " geniculation " of the pedicle valve (Pl. 6, fig. 7). On *P. plicatilis* ribbing occurs with a frequency of 8, 9 and 10 ribs per 5 mm. width on 3, 3 and 2 pedicle valves just anterior of the last ruga. They are similarly developed on brachial valves. Exfoliation of the brachiopod shell exposes younger shell substance, commonly deposited in a similar way to deposition at the growth margin at that particular stage, or mimicking the surface immediately covering that area, according to the depth of exfoliation. Thus ribbing seen on an exfoliated surface, as admitted by Thomas (1914 : 333) might be expected to show at the surface, either at that place, or more anteriorly. As the present material is silicified, it is impossible to be dogmatic about the occurrence of exfoliation, however, it is unlikely to have occurred as spines are commonly retained and the rugae well formed and sharp. It is unlikely that abrasion occurred in the interrugal spaces, or deep within the concavity of the shell, at the point of the brachial valve geniculation ; places where ribbing can be well seen. For these reasons it is believed that the ribbing was developed primarily, at the shell margins during the greater part of growth, and that it is of diagnostic importance.

The brachial impressions are described for the first time. In *P. plicatilis* they are lobate, extending antero-laterally from between the anterior and posterior adductor scars at about 60° to the mid-line, and extending almost to the antero-lateral corners of the visceral disc. They extend about two-thirds of the valve length and about one-half of their own greatest width (Pl. 6, fig. 15). The enclosing ridges are low and broad, are best seen posteriorly, and the rugation within the areas enclosed is somewhat blurred.

Plicatifera plicatilis (J. de C. Sowerby)

(Pl. 6, figs. 6–15 ; Pl. 7, figs. 1–18 ; Text-fig. 8)

1824 *Producta plicatilis* J. de C. Sowerby : 85, pl. 459, fig. 2.
1914 *Pustula plicatilis* (J. de C. Sowerby) Thomas : 331, pl. 20, fig. 22.
1927 *Plicatifera plicatilis* (J. de C. Sowerby) Chao : 25.
1928 *Productus pseudoplicatilis* Muir-Wood : 189, pl. 11, figs. 17*a–e*.

EMENDED DIAGNOSIS. Subrectangular, length about one-half maximum width, at or equal to width of hinge-line, ears broadly convex, umbonal slopes gentle ; profile unequi-concavo-convex to plano-convex, curvature slight over rugate regions ; pedicle valve gently geniculated with long curved and slightly sulcate venter and trail ; thickness about equal to length, body cavity deep ; radial ornament forming slight, uneven reticulation with stronger rugae, and continuing beyond on to non-rugate region ; about 9 ribs in 5 mm. width, anterior of rugae ; about 24 prominent and regular rugae cover one-half pedicle valve length and whole brachial valve, except trail ; growth lines distinct on smooth venter and prominent on trail ; spines sparsely developed but strong ; clasping spines and pedicle sheath on juvenile valves, adult pedicle valves with about six ill-defined radial rows of 2 or 3 spines set on rugae, rows continued on lateral and antero-lateral smooth flanks ; ventral adductor field nearly one-half valve length and two-fifths as wide as long ; diductor scars extending slightly beyond adductor scars ; cardinal process distinctly bilobed in young, lobes medianly fused in adult, myophores postero-dorsally directed ; adult lateral ridges strong, extending beyond hinge-line on to flanks of cardinal process and anteriorly diverging from hinge-line at about 15°, extending round inside of ears to lateral margins where they are externally crenulated ; adductor field raised, extending about one-third valve length and wider than long, divisible into trigonal and lobate anterior and posterior scars ; median septum about two-thirds valve length, high anteriorly ; brachial impressions from between anterior and posterior adductor scars, at about 60° to mid-line, lobate, ridges low ; trail tuberculate.

MEASUREMENTS (in mm.)	length	width
Complete pedicle valve (BB.52832)	15·0	19·4
Complete brachial valve (BB.52833)	14·0	25·8
Pedicle valve interior } paired valves { (BB.52834) .	—	23·0
Brachial valve interior (BB.52835) .	14·0	21·0
Brachial valve (BB.52836)	5·7	8·3
Shell with broken pedicle valve (BB.52837) . . .	14·5	19·1
Complete pedicle valve (BB.52841)	0·7	0·9
Complete pedicle valve (BB.52842)	1·8	2·1
Incomplete pedicle valve with bryozoan (BB.52843) .	—	2·5
Complete pedicle valve (BB.52844)	3·1	4·2

LOCALITY AND HORIZON. Subreefal limestones, Bunnahone, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. Of the three specimens of *Producta plicatilis* in the Sowerby Collection only one, B.M. (N.H.) B.60960, was figured by Sowerby (1824, pl. 459, fig. 2). This specimen was designated as lectotype by Thomas (1914 : 332) and the Fermanagh shells agree with it in all known respects, such as outline, profile, rugation and ribbing. The type specimen is about one-half the width of the other Sowerby specimens and these have about 28 rugae on each valve (cf. Table 9) but show no sign of ribbing. These two large specimens clearly differ from the type, possibly because of a differing environment, and may not be conspecific. There is a wide variation of size and development of the antero-ventral sulcus in specimens from different localities and it remains to be seen whether the ribbing is associated with other characteristics warranting specific distinction.

A comparison of the type specimen of *Plicatifera plicatilis* with the holotype of *P. pseudoplicatilis* Muir-Wood reveals that the two are conspecific and it is possible that Muir-Wood's comparison (1928 : 190) was based upon the two large Sowerby specimens. The only differences seen in these type specimens are that *P. pseudoplicatilis* has no sulcation and the brachial valve geniculation is slightly less than in *P. plicatilis*. However, these differences are covered by specific variation.

There is no true geniculation in the pedicle valve of *P. plicatilis* and its even convexity can be seen illustrated by Thomas (1914 : 331, text-fig. 13). Towards its anterior margin the brachial valve is commonly geniculated against the inner surface of the pedicle valve.

P. plicatilis is unusual in the depth of the body cavity, which in adult shells is over one-half of the length. The pedicle valve rugation stopped after the development of about 24 rugae, at the lowest, or most ventral part of the valve and immediately posterior to the " geniculation ". (It is commonly impossible to see the posterior three or four rugae because of abrasion to the ventral umbo.) At this stage the brachial valve did not form a trail against the pedicle valve, but continued to rotate dorsalwards around the hinge-line, so that the body cavity increased in depth until

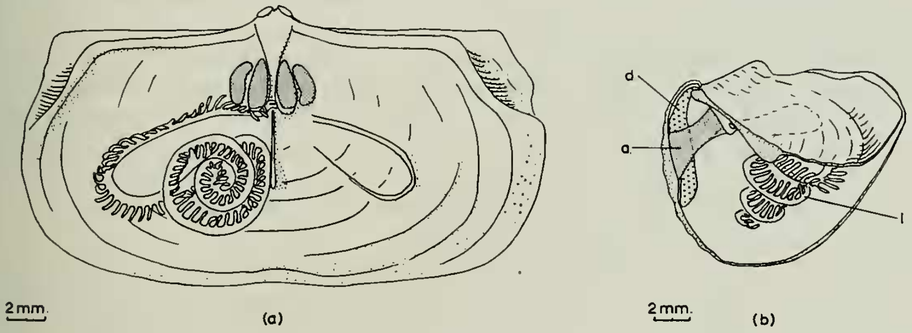

FIG. 8. Illustrations of (a) the brachial valve interior showing the adductor muscle scars, the inferred position of the stylized lophophore, and the postero-lateral crenulations across the inner margins of the ears ; (b) an internal lateral view of a stylized reconstruction of *Plicatifera plicatilis* (J. de C. Sowerby) ; *a*, adductor muscles ; *d*, diductor muscles ; *l*, stylized lophophore.

the dorsal visceral disc was at about 70° to the rugate portion of the pedicle valve. Thus the rugation only extends for about one-half the full length of the ventral visceral region, the rest being smooth with faint ribbing, and it is somewhat misleading to describe all the smooth region as a trail. As the dorso-anterior curvature of the pedicle valve formed the arc to the rotating brachial valve, growth in the latter was confined to extension of the developing trail, and was probably slower than that of the pedicle valve.

P. plicatilis was furnished with a pedicle sheath in its earliest stages of growth (Pl. 7, figs. 1, 4) and at a length of about 2 mm. the ventral valve had three pairs of clasping spines which arched over the beak. The first pair was developed on the brephic valve, lateral to the shallow groove extending antero-ventrally from the pedicle sheath, and formed a circle of about 0·2 mm. in diameter. Rarely, thin fragments of bryozoans are preserved held by these spines (Pl. 7, fig. 3). The second pair developed close to the hinge-line, about 1·0 mm. apart, and curved to form a ring, commonly in contact with the posterior circumference of the first ring (Pl. 7, fig. 12), unless deflected by some foreign object. The third pair, again close to the hinge-line, developed about 1·8 mm. apart, at a valve length of about 1·4 mm. and curved postero-ventrally, commonly to within 0·5 mm. of the valve surface, but less regularly than the previous spines because of deflection against solid objects, usually the object held by the preceding spines and used as anchor by the young shell (Pl. 7, figs. 7, 8). By this stage a pair of normal antero-ventrally directed sub-erect spines, and a single median spine, had developed. All subsequent spines were of this type and developed more or less symmetrically in pairs from the crests of the rugae. However, both spines of a pair were not always situated on the same ruga, and the spacing became more widely separated anteriorly. On the flanks of the adult smooth region two rows of three or four laterally directed spines developed, together with one or two pairs of anteriorly directed spines.

The ventral adductor scars are evident in valves about 6 mm. long but are not easily distinguishable from the diductor scars. By adulthood, when the non-rugate anterior region had developed, the adductor scars were distinctly raised. The dorsal adductor scars became defined at an earlier stage and can be seen in valves of only 2 mm. long. The raised, elongately oval to trigonal, anterior scars developed first. The posterior scars only became visible in adulthood, at first as tuberculate ridges flanking the anterior scars, but later as raised pear-shaped or trigonal areas a little shorter than, and lateral to the anterior scars. Both scars are rather variable in detail, but the complete field is commonly a little over three-quarters as long as wide and about one-third as long as the visceral disc.

The median septum developed between the adductor scars from a valve length of about 6 mm. In adult shells, 11 to 12 mm. long, the septum is two-thirds the valve length, but is completely buried by secondary shell for most of its length between the adductor scars. It reached its greatest height, of about 1 mm., anteriorly, between the brachial impressions, and is marginally thickened. Posteriorly a wide ridge of secondary shell connects the adductor platform to the base of the cardinal process and to the median ends of the lateral ridges (Pl. 6, fig. 15).

The juvenile cardinal process is distinctly bilobed, but fused ventro-medianly over a deep alveolus which penetrates almost to the dorsal beak and represents the inside of the protegulal node (Pl. 6, fig. 12). Indeed, the internal distinction of the lobes is so complete that it seems clear that the cardinal process grew from a rudiment at the posterior end of the protegulal node as two elevated ridges, supported by the rudiments of the lateral ridges, which were enlarged antero-ventrally to cover the cavity postero-ventrally. Posteriorly, along either side of the nodal cavity, the lobes were fused and formed an arch together with the median ends of the lateral ridges. From this arch the incised myophore lobes extended ventrally, separated by a deep sulcus (Pl. 6, fig. 11). Continued shell deposition at the edges of the myophores, around the muscle bases, caused them to become both increasingly deeply incised and the progressive fusion of the two median muscle boundaries with one another. This fusion occurred at variable stages of growth, and the cardinal process commonly remained distinctly bilobed until adulthood, and only then were the inner, or ventral, margins of the lobes united medianly. Also at this stage, the deposition of secondary shell, anterior to the cardinal process, filled the alveolus, the remnant of the protegulal body cavity.

The lateral ridges began development in valves 4 to 5 mm. long, and diverged from the hinge-line at 15°. During growth they became increasingly prominent, extending over one-half the distance to the cardinal extremities by the time the rugate region of the pedicle valve was developed. Subsequently, curvature of the pedicle valve increased and the externally crenulated ridges across the insides of the ears developed. When the visceral disc had attained a width of 20 mm. the ridges had fused with these ear ridges (" ear baffles " of Muir-Wood) to form a continuous ridge from the cardinal process to the widest part of the visceral disc on the lateral margins. As the brachial valve rotated dorsally during growth these ridges became increasingly prominent and maintained a sealed posterior margin, and articulatory surfaces. The ridges became deeply concave posteriorly for the reception of the angular lateral ridges which had developed simultaneously within the pedicle valve (Pl. 7, fig. 18). The crenulations on their outer surfaces, at the postero-lateral margins, became marked and fitted those similarly placed on the flanks of the pedicle valve interior. In the pedicle valve, the traces of these crenulations indicate the brachial valve rotation during growth, not the amount of possible movement of the brachial valve in life.

TABLE 7

$\overline{L}$ mm. (var.) = 8·66 (17·006)	$\overline{Ad.L}$ mm. (var.) = 2·51 (1·867)
$\overline{W}$ mm. (var.) = 15·48 (75·196)	$\overline{Ad.W}$ mm. (var.) = 3·14 (2·974)
r = 0·983	r = 0·997
a (var.) = 2·103 (0·0250)	a (var.) = 1·262 (0·00166)

TABLE 7. Statistics of length (L), maximum width (W), length of adductor scars (Ad.L), and width of adductor scars (Ad.W) of 8 brachial valves of *Plicatifera plicatilis* (J. de C. Sowerby).

TABLE 8

$$\bar{L}\ \text{mm. (var.)} = 5{\cdot}90\ (16{\cdot}220)$$
$$\bar{W}\ \text{(var.)} = 9{\cdot}04\ (51{\cdot}363)$$
$$r = 0{\cdot}986$$
$$a\ \text{(var.)} = 1{\cdot}779\ (0{\cdot}01267)$$

TABLE 8. Statistics of length (L) and width (W) of 9 pedicle valves of *Plicatifera plicatilis* (J. de C. Sowerby).

TABLE 9

Number of rugae	20	21	22	23	24	25	26
Number of specimens	1	0	2	6	4	3	2

TABLE 9. The number of rugae counted on 18 pedicle valves, in which all the rugae had developed, of *Plicatifera plicatilis* (J. de C. Sowerby).

Subfamily **PRODUCTININAE** Muir-Wood & Cooper 1960

Genus ***PRODUCTINA*** Sutton 1938

1928 *Thomasia* Fredericks : 790.
1931 *Thomasina* Paeckelmann : 181.
1938 *Productina* Sutton : 551.
1942 *Thomasella* Paul : 191.
1951 *Argentiproductus* Cooper & Muir-Wood : 195.
1960 *Argentiproductus* Cooper & Muir-Wood ; Muir-Wood & Cooper : 182.

EMENDED DIAGNOSIS. Outline subsemicircular to suboval, hinge-line straight, commonly widest part of shell, umbo prominent ; profile strongly concavo-convex with narrow body cavity ; costae commonly prominent on pedicle valve, rarely branching dichotomously, widening and flattening towards anterior margin and bearing suberect spines posteriorly ; strong spine rows across umbonal slopes towards postero-lateral margins, and more or less symmetrically placed spines postero-medianly ; concentric lamellae, prominent on brachial valve which is obscurely ribbed ; ventral adductor scars elongately trigonal, slightly raised ; diductor scars indistinct, flabellate ; lateral ridges diverging from umbo across anterior margins of ears ; cardinal process sessile but strongly bilobed, each lobe dorso-posteriorly incised ; lateral ridges diverging from flanks of cardinal process at low angle from hinge-line ; adductor scars trigonal to elongately oval, slightly raised; median septum ill-defined, not fused to base of cardinal process, about three-fifths valve length.

Type species. *Productus sampsoni* Weller 1909, by original designation of Sutton (1938 : 551).

Discussion. The present material was collected from beds of approximately the same stratigraphic position, and 12 miles north-west of the locality in Co. Fermanagh from which Phillips collected *Producta margaritacea* the type species of *Argentiproductus* Cooper & Muir-Wood 1951. Despite obvious external similarities with *Argentiproductus*, as conceived by Muir-Wood & Cooper, (1960 : 182), the dorsal interiors actually agree more closely with those of *Productina* Sutton from which they differ only in their greater size. Moreover Sutton (1938 : 551) states that *P. margaritacea* may be congeneric with his genus. Weller's original description of the type species, *Productus sampsoni*, gives no information about internal morphology, but there is no doubt that all the specimens referred to by him were no more than 13 mm. long. Their outline is perhaps more rounded than that of *P. margaritacea*, but the cardinal extremities of all specimens illustrated by Weller and by Muir-Wood & Cooper appear to be broken, so that they may, in fact, be more transverse than is stated. The two genera, *Productina* and *Argentiproductus*, are distinguished by Muir-Wood & Cooper (1960 : 182) on characteristics that vary with size, such as the width of ribbing, the convexity of the shell, etc. together with more important differences between the dorsal interiors. The dorsal interior of *Argentiproductus* figured by them (pl. 123, figs. 17, 17*a*), however, is of a brachial valve from Visé, Belgium and is quite unlike the interiors of brachial valves in the Fermanagh fauna. On the other hand, the illustrated dorsal interior of *Productina* (*P. sampsoni*, pl. 123, figs. 7, 9) is closely comparable to interiors of immature Fermanagh valves (Pl. 8, fig. 9). It seems, therefore, that the dorsal interior attributed to *Argentiproductus* does not belong to the type species of that genus, and the American and British species do not warrant separation at generic level.

Productina margaritacea (Phillips)

(Pl. 8, figs. 1–19; Pl. 15, figs. 1–8)

1836 *Producta margaritacea* Phillips : 215, pl. 8, fig. 8.
1861 *Productus margaritaceus* Phillips; Davidson : 159, pl. 44, figs. 5–8.
1951 *Argentiproductus margaritaceus* (Phillips) Cooper & Muir-Wood : 195.
1960 *Argentiproductus margaritaceus* (Phillips); Muir-Wood & Cooper : 182, pl. 123, figs. 11–16, *non* fig. 17.

Emended diagnosis. Outline subsemicircular with widest point at or near straight hinge-line, length about three-fifths width, umbo arched, rounded and extending well beyond hing-line, lateral slopes steep, ears narrowly tringular; adult profile strongly concavo-convex, depth about one-half length; ribs more prominent on pedicle valve, low flattened anteriorly with narrow interspaces, about 6 per 2·5 mm., 4 mm. antero-medianly from ventral umbo; concentric ornament lamellose, prominent on brachial valve, variable on pedicle valve ; young with pedicle-sheath from ventral beak ; spines posteriorly confined ; prominent rows of about five spines along each umbonal slope and anterior to ears, commonly one or two median spines, others sparsely paired within first 8 mm. of length, ventral adductor scars slightly raised, lanceolate to elongately trigonal, flanked by rounded, elongately trigonal anteriorly spreading diductor scars ; articulatory ridges diverge from umbo at about 20° to hinge-line and die out laterally across anterior margin of ears ; prominent lateral spines retain internal connections ; cardinal process sessile but prominently bilobed, each myophore incised forming V-shaped, quadrifid postero-dorsally directed surface ; supporting ridges diverge from hinge-line at about 30° for about one-half hinge width ; adductor scars rounded trigonal, about as long as wide and extend one-third valve length, slightly raised, especially in young ; median septum ill-defined, arising between adductor scars and extending over one-half adult length ; median and anterior surfaces of valves tuberculate, shell substance pseudopunctate.

MEASUREMENTS (in mm.) :	length	width
Incomplete shell (BB.52904)	17·3	—
Incomplete shell (BB.52905)	14·3	20·2
Incomplete pedicle valve (BB.52906)	*c.* 8·0	*c.* 12·0
Incomplete pedicle valve (BB.52907)	*c.* 7·3	*c.* 10·0
Incomplete pedicle valve (BB.52908)	—	*c.* 9·0
Complete brachial valve (BB.52909)	13·0	22·8
Complete brachial valve (BB.52910)	3·0	5·2
Incomplete brachial valve (BB.52911)	1·8	*c.* 2·8
Complete pedicle valve (BB.52912)	4·1	6·0
Incomplete pedicle valve (BB.52913)	2·4	*c.* 3·8
Incomplete pedicle valve (BB.52914)	3·4	3·8
Incomplete pedicle valve (BB.52915)	1·9	—

LOCALITIES AND HORIZON. Subreefal argillaceous limestone at Bunnahone and Carrick Loughs, about 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. Disarticulated valves and shells ranging from under 2 mm. to about 20 mm. in length provide ample material for ontogenetic studies. During larval settlement onto a suitable substratum, which was probably firm or solid, the protegulal node developed as a bilobed structure about 0·3 mm. in length, from the posterior end of which was secreted a narrow pedicle sheath (Pl. 8, fig. 18). From the postero-ventral surface of this shell rudiment was developed the brephic valve, commonly about 1·0 mm. long and 0·75 mm. wide, with a postero-ventrally directed longitudinal groove across its length, inherited from the bilobate protegulum. One or two pairs of spines within 0·5 mm. of the pedicle sheath, and 0·2 to 0·3 mm. apart, formed complete encircling rings over the groove (Pl. 15, fig. 6). These spines are thought to have grown in this way as a genetically controlled feature rather than in response to the form of the substratum, but in some larvae they might have encircled erect cylinders like spines in a productoid colony when chance settlement afforded such a substratum. In any event, the pedicle rudiment was soon lost because its internal opening became sealed at about this stage of growth, as can be seen in one valve, 2 mm. long. This closure is unlikely to have been due to silicification because openings to the nearby encircling spines are marked by distinct depressions.

The external groove is represented internally by a ridge which was continued during valve growth as low adductor platforms, but which was distinguishable as such only in valves about 2 mm. long. At this stage the diductor scars are elongately trigonal and rounded, extending anteriorly of the adductor scars along the insides of the umbonal slopes (Pl. 8, fig. 16).

The onset of neanic growth stages is shown in valves between 0·8 and 1 mm. long by a prominent growth-line and by the first pair of laterally directed spines. The radial ornamentation was initiated at this stage, but is seldom visible until the valves attained a length of 1·5 to 2 mm. Commonly at a length of just over 1 mm., a second pair of spines arose on either side of the mid-line, near the first median spine, which is anteriorly directed, and just before the formation of the first pair of longer spines on the umbonal slopes. These are the first of the two rows of spines flanking the umbo and front of the ears. Subsequent growth continued with the periodic development of symmetrically placed paired spines, and occasional median spines, in such a way that the increase of valve area led to a reduction of spine density towards the anterior margin. With the exception of the row of strong flanking spines (and a single median spine which was commonly developed 8 mm. from the umbo), the spines ceased to grow in valves more than 4 mm. long so that the total number of spines, excluding the brephic ones, is about eighteen. Strictly speaking the first formed pair of laterally directed spines on the neanic shell should probably be included as members of the rows of flanking spines. This has not been done on the measured specimens as it was frequently impossible to locate their position accurately, which is about 0·4 mm. from the beak (Table 12). All the spines arose as a thickening and anterior prolongation of a rib crest and are at an angle of less than 60° to the valve surface.

Internally, the laterally directed ridges which demarcate the anterior extremities of the ears, grew to about three-fifths of the valve width. In so doing they sealed the internal openings of the more medianly placed flanking spines so that only the younger one or two pairs retained their internal connections, and hence their powers of growth.

Brachial valves are furnished with a small oval protegulal node, about 0·3 mm. long, and a rounded, smooth brephic valve about 0·8 mm. long. Beyond this length low lamellose concentric ridges were formed across which the indistinct ribs can be traced. There are no spines. In valves of 1·8 mm long, the adductor scars are prominent as slightly raised oval markings reaching nearly one-half the valve length (Pl. 15, fig. 8). The lateral ridges diverge from the hinge-line at about 20° and extend for one-half of its width, i.e. about 0·6 mm. on either side of the distinctly bilobed cardinal process. The posterior growth of the cardinal process, together with that of the median ends of the lateral ridges, extended the latter beyond the hinge-line when the valve was about 3 mm. long. By adulthood the ridges extended about half way up the flanks of the cardinal process and are externally visible for approximately one-fifth of the hinge width. These ridges not only supported the cardinal process, but more importantly aided the articulation of the valves and are essentially the same structures as the socket ridges of the Strophalosiidae. They form wide flat areas, lateral to the cardinal process, against which the more medianly placed parts of the lateral ridges of the pedicle valve articulated (Pl. 8, figs. 8–9).

The median septum is never strongly developed and arose at a valve length of about 3·0 mm. as a low ridge about 1 mm. long and extending for two-thirds of the valve length. It grew from a point between the anterior ends of the adductor scars and during growth extended posteriorly between the scars and slightly anteriorly to a distance of just over one-half the valve length. The septum never seems to have fused to the base of the cardinal process. While remaining distinct during growth, the adductor scars became less raised because of the surrounding deposition of secondary shell.

The strong curvature of the pedicle umbo commonly protected it from abrasion so that even adult shells, about 18 mm. long (measured as a chord to their curvature), may retain the stumps of the brephic spines and pedicle sheath.

The radial ornamentation is more prominent on pedicle valves than brachial valves, where the lamellose ornamentation is more pronounced. An increase in the number of the ribs is by rare dichotomy, largely confined to the posterior spinose region. All ribs increase in width towards the anterior margin by four or five times their original width, and become increasingly flat topped. The interspaces always remain narrower than the ribs. Dichotomy commonly occurred posterior to one of the lamellae. However, the dichotomy commonly did not continue beyond the lamella, and here the rib may once again be single. In this way a rib may have formed several incipient branchings, by the division of the fold at the anterior margin of the mantle, which were suppressed by the retraction of the mantle which formed the lamellae. Commonly the renewed forward growth of the mantle continued in the prebranched condition so that a single rib formed at the valve surface. Thus, the number of ribs at the anterior margin of a shell is usually less than would be expected from the number of incipient branchings that occurred along the costae.

TABLE 10

$\overline{L}$ mm. (var.) = 7·45 (25·075)
$\overline{W}$ mm. (var.) = 11·03 (66·876)
r = 0·991
a (var.) = 1·633 (0·00185)

$\overline{L}$ mm. (var.) = 7·45 (25·075)
$\overline{Th}$ mm. (var.) = 3·08 (5·589)
r = 0·911
a (var.) = 0·472 (0·00146)

TABLE 10. Statistics of length (L), width (W) and thickness (Th) of 28 pedicle valves of *Productina margaritacea* (Phillips).

TABLE 11

Ribs	4	5	6	7	8	9
At 4 mm.	0	1	8	5	6	1
At 6 mm.	3	5	5	1	0	0

TABLE 11. Ribs counted per 2·5 mm. width at 4 mm. and 6 mm. antero-medianly from the ventral umbo of *Productina margaritacea* (Phillips).

TABLE 12

Mid-line to	1st spine	2nd spine	3rd spine	4th spine	5th spine
Mean (mm.)	0·90	1·72	3·40	8·30	12·73
(var.)	0·010	0·0984	0·6711	6·5933	11·53
N	25	27	21	5	3

TABLE 12. Statistics of distances from the mid-line to the first, second, third, fourth and fifth spines on the line of prominent spines flanking the umbonal slopes to the postero-lateral margins of *Productina margaritacea* (Phillips). (A neanic pair of spines at about 0·4 mm. from the mid-line should perhaps be included in this series.)

TABLE 13

$\overline{\mathrm{L}}$ mm. (var.) = 3·67 (6·183)
$\overline{\mathrm{W}}$ mm. (var.) = 6·24 (20·820)
r = 0·995
a (var.) = 1·835 (0·0020)

$\overline{\mathrm{L}}$ mm. (var). = 3·67 (6·183)
$\overline{\mathrm{AdL}}$ mm. (var.) = 1·22 (0·427)
r = 0·950
a (var.) = 0·276 (0·00044)

$\overline{\mathrm{AdL}}$ mm. (var.) = 1·22 (0·472)
$\overline{\mathrm{AdW}}$ mm. (var.) = 1·41 (0·365)
r = 0·983
a (var.) = 0·897 (0·00155)

TABLE 13. Statistics of length (L), maximum width (W), length of the adductor scars from the hinge-line (AdL) and their total width (AdW) in 19 brachial valves of *Productina margaritacea* (Phillips).

TABLE 14

$\overline{\mathrm{L}}$ mm. (var.) = 5·53 (16·411)
$\overline{\mathrm{MsL}}$ mm. (var.) = 2·90 (4·139)
r = 0·969
a (var.) = 0·502 (0·00153)

TABLE 14. Statistics of length (L) and length of the median septum (MsL) from the hinge-line of 12 brachial valves of *Productina margaritacea* (Phillips).

Family **OVERTONIIDAE** Muir-Wood & Cooper 1960

Subfamily **OVERTONIINAE** Muir-Wood & Cooper 1960

Genus ***OVERTONIA*** Thomas 1914

TYPE SPECIES. *Producta fimbriata* J. de C. Sowerby 1824, by original designation of Thomas (1914 : 259).

Overtonia fimbriata (J. de C. Sowerby)

(Pl. 9, figs. 1–13 ; Pl. 10, figs. 1–7 ; Text-fig. 9)

1824 *Producta fimbriata* J. de C. Sowerby : 85, pl. 549, fig. 1.
1861 *Productus fimbriatus* J. de C. Sowerby ; Davidson : 171, pl. 33, figs. 12–15 *non* pl. 44, fig. 15.
1914 *Overtonia fimbriata* (J. de C. Sowerby) Thomas : 259, 335, pl. 20, figs. 12–17.
1960 *Overtonia fimbriata* (J. de C. Sowerby) ; Muir-Wood & Cooper : 183, pl. 46, figs. 10–20.

EMENDED DIAGNOSIS. Outline subrounded, length of adult shell almost equal to maximum width, commonly at mid-length, umbo rounded extending well beyond straight hinge-line which commonly forms maximum width of young shells ; ears small triangular ; profile subsemicircular, plano-convex to slightly concavo-convex, a little over one-half as deep as long, body cavity deep, short dorsally directed trail ; concentric rugae rounded and prominant posteriorly, becoming wider, flatter and increasingly lamellose anteriorly ; about three high-angled, antero-ventrally directed spines per 5 mm. at 5 mm. antero-medianly of ventral umbo ; from about sixth ruga, and anterior to each spine, lamellae tightly folded into prostrate spine-like extensions projecting between spines of anterior ruga, so forming longitudinally disposed short ridges between spine rows ; growth-lines well developed between rugae ; brachial valve almost flat across disc, geniculated against pedicle valve, ornamented by closely spaced concentric lamellae and low rugae bearing more closely spaced dorsally directed spines ; rugae forming acute angle with hinge-line towards cardinal extremities ; ventral interior poorly developed and preserved, ridges diverging narrowly from beak and extending at low angle from hinge-line towards inner margins of ears ; muscle field indistinct, adductor scars elongately trigonal with more rounded, spreading diductor scars ; anteriorly tuberculate and with spine openings ; two lobes of cardinal process more or less fused dorsally but separated by groove ventro-posteriorly, myophores deeply incised to tube-like ; lateral ridges diverging from base of cardinal process at 20° to hinge-line and extending round inside of ears to form low visceral ridge around disc ; adductor platform prominently raised, postero-ventrally facing, divisible into elongately trigonal anterior scars and small trigonal posterior scars, whole muscle field about twice as wide as long ; median septum short, prominent anteriorly as bulbous prolongation, about one-third valve length ; brachial impressions from anterior flanks of adductor platform, antero-laterally to anteriorly directed, lobate ; strongly tuberculate anteriorly ; shell substance pseudopunctate.

Measurements (in mm.)	length	width
Complete shell (BB.52845)	16·5	17·0
Complete pedicle valve (BB.52846)	14·3	15·8
Complete brachial valve (BB.52847)	11·9	15·0
Complete brachial valve (BB.52849)	8·2	9·0
Complete shell (BB.52850)	9·6	10·5
Complete shell (BB.52851)	5·6	6·2
Incomplete brachial valve (BB.52848)	10·5	14·5

Locality and horizon. Subreefal limestones, Bunnahone, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

Discussion. The type specimen of *O. fimbriata* (J. de C. Sowerby) is apparently lost (Thomas 1914 : 339) and the two specimens in the Sowerby Collection (B.M.N.H., No. 60978–79) named *Producta fimbriata* are thought to be misidentified. Neither of these specimens match Sowerby's (1824 : 85) description or figure and one (B.60978) is probably an echinoconchid, while the other (B.60979) is probably *Overtonia* but not *O. fimbriata*. Both are poorly preserved and not localized. Thomas (1914 : 259) based his generic description of *Overtonia* upon several specimens, making special reference to material in the Davidson Collection (B.M.N.H. Nos. B.5762, B.13854), but he did not designate a neotype. In his specific description of *O. fimbriata* Thomas said that the Davidson specimens (B.13854) were typical and should it become necessary to stabilize nomenclature by the designation of a neotype, it is from these specimens that it should be chosen.

Thomas (1914) noted that the greatest width in young shells may temporarily be at the hinge-line and that the length of the pedicle valve is slightly greater than its maximum width. In the present sample the width is greater than the length indicating the variation which can occur between these attributes within the species as a whole (Table 16). There is a high correlation between length and depth and these dimensions display an allometric relationship resulting from the high degree of curvature of the pedicle valves, which in adult specimens is more than 360°.

A young pedicle valve, about 9·0 mm. long shows a shallow umbonal groove, flanked by a pair of spine bases. There are signs of a pedicle sheath on this specimen, as also on a few other pedicle valves.

Ornamentation is distinctive. On pedicle valves the rugae became increasingly spaced during growth and the spines, which arose from the rugae, more widely separated, so that few spines were added beyond a shell length of about 5 mm. Within a width of 5 mm., 3 and 4 spines were counted in 9 and 3 pedicle valves respectively at a distance of 5 mm. antero-medianly of the ventral umbo. The spines extended anteriorly at about 60° to the valve surface, but soon increased their curvature to reduce this angle. They are radially arranged, but miss every second ruga, so that they form two diagonal sets at 35° to 40° from one another (Pl. 9, fig. 4). Commonly the sixth and subsequent rugae became anteriorly lamellose and developed tight radially arranged folds anterior to each spine. These folds formed spine-like ridges that extended anteriorly from the spines of one ruga to a point between the spines on the next anterior ruga (Pl. 9, figs. 2, 4). Thomas (1914 : 335) and Muir-Wood & Cooper (1960 : 184) refer to " spine bases " or " spine ridges " without mentioning the antero-dorsally directed, lamellose spine-like projections with which they are associated. The ridges are not the spine bases for the normal erect spines. However, Thomas was correct in stating that the " spine bases " occasionally extend across " the depresssions between the rugae " but are never sufficiently continuous to form true costation ". It is, in fact, clear that a costation could not have been formed by these ridges because of their en-echelon arrangement, and that Muir-Wood & Cooper (1960 : 184) erred in saying that these spine ridges extend " across bands or from one band to the next, thus simulating costae ".

The brachial valves are similarly ornamented, except that the concentric lamellae and spine rows are more closely spaced. This is because their total number is the same as on the corresponding pedicle valve, while the surface length of the valve is considerably less (Text-fig. 6). There are 5 or 6 spines in 5 mm. width, 5 mm. from the dorsal umbo. The lamellae are not folded into spine-like ridges, as on the pedicle valve.

Internally the brachial valve shows a number of unusual features. The two lobes of the cardinal process are medianly fused for most of their length so that the myophores are narrowly V-shaped but very deeply incised. The area of attachment of the diductor muscle bases must, therefore have been strongly arcuate so that

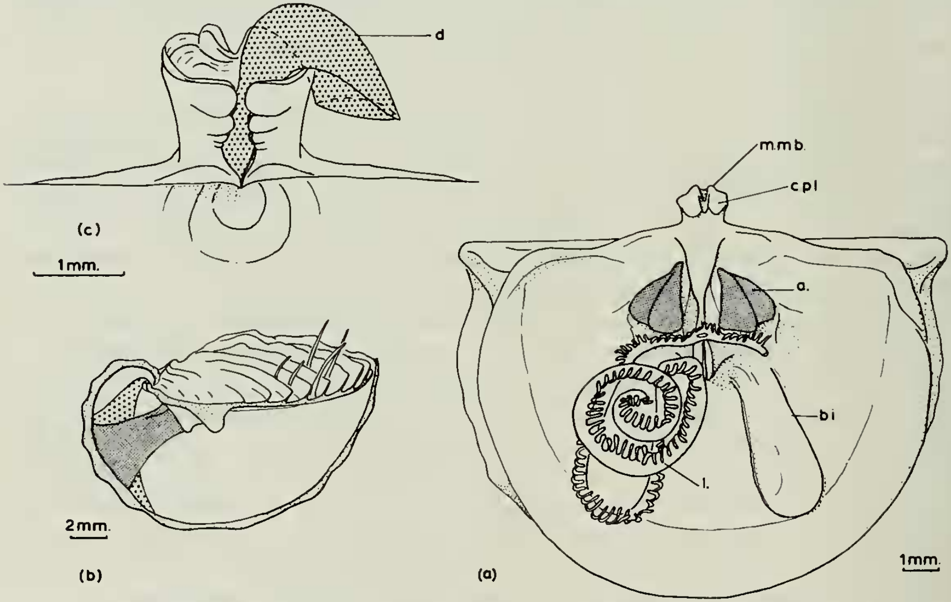

FIG. 9. Illustrations of (a) brachial valve interior ; (b) lateral view of shell interior and (c) external view of cardinal process, with the diductor muscle attached to one lobe, of *Overtonia fimbriata* (J. de C. Sowerby) *a*, divided adductor scars ; *b.i*, brachial impressions ; *c.p.l.*, cardinal process lobe ; *d*, diductor muscle extending from cardinal process towards the floor of the pedicle valve ; *l*, stylized lophophore ; *m.m.b*, median muscle boundary.

shell deposition formed open-sided tubes, the sides opening dorso-medianly down the centre of the dorsal surface of the cardinal process along a common groove (Pl. 9, figs. 6–8). The diductor muscles extended from the posterior ends of these tubes and curved ventrally to the floor of the pedicle valve (Text-fig. 9, *c*). Internally the two lobes are more widely separated and, where they fused proximally, there are two small ventrally directed nodes.

The adult dorsal adductor field faces postero-ventrally at about 60° to the commissural plane, so that its anterior margins are built up by a thick deposit of secondary shell (Pl. 9, figs. 8, 9). This high degree of tilting was presumably in response to the unusually deep body cavity, which was accentuated during growth by the dorsal rotation of the brachial valve about the hinge-line. The tilt of the adductor platform maintained the muscle scars more or less parallel to the ventral adductor scars and allowed these muscles to retain a higher degree of efficiency than would otherwise have been possible (Text-fig. 9, *b*).

Between, and anterior to, the adductor platform, and divided by the median septum, is a deep triangular to rhomboidal area which has been likened to that found in a similar position in *Leptagonia analoga* (Davidson 1861 : 172). It seems likely that these depressions on either side of the median septum housed the trunks of the *vascula media*. The median septum itself is much enlarged anteriorly, while posteriorly it is covered by shell substance between the posterior margins of the adductor platforms. In a young valve 8 mm. long, the adductor platforms are free of the valve floor anteriorly, and below their arching anterior margins can be distinguished antero-laterally directed probuberances which project immediately above, and in line with, the outer margins of the faint brachial impressions (Pl. 10, fig. 3). These protuberances may have supported the median, oral segment of the lophophore, before the full growth of the cardinalia, by which time they had become covered by shell supporting the adductor platforms. In the adult shell, the lophophore was probably attached to the anterior edge of these platforms, the mouth being between their anterior margins and ventral to the median septum. The lophophore continued around the brachial markings to curve medianly and anteriorly onto the prominent anterior end of the median septum. From this point two spires probably hung into the deep pedicle valve (Text-fig. 9). This arrangement necessitates the final free spires to have been coiled in the opposite sense to those suggested for *Productus* s.s. by Williams (1956, text-fig. 5 (6)).

TABLE 15

No. of rugae	6	7	8	9	10	11	12	13	14
No. of specimens	3	2	1	2	1	5	0	0	1
Approx. length of of specimens	6	8·5	11·5	12·0	13·0	14·0	—	—	17·0

TABLE 15. The number of rugae counted on 15 pedicle valves of *Overtonia fimbriata* (J. de C. Sowerby), together with the approximate length of the valves at each additional ruga.

TABLE 16

$\overline{L}$ mm. (var.) = 11·38 (12·349)
$\overline{W}$ mm. (var.) = 12·63 (15·005)
r = 0·986
a (var.) = 1·102 (0·00262)

$\overline{W}$ mm. (var.) = 12·63 (15·005)
$\overline{HiW}$ mm. (var.) = 11·33 (11·088)
r = 0·949
a (var.) = 0·860 (0·00563)

$\overline{L}$ mm. (var.) = 11·38 (12·349)
$\overline{Th}$ mm. (var.) = 6·04 (5·384)
r = 0·992
Log$_e$ $\overline{L}$ (var. log$_e$ L) = 2·388 (0·908)
Log$_e$ $\overline{Th}$ (var. log$_e$ L) = 1·729 (0·1381)
r_e = 0·997
α (var.) = 1·229 (0·00070)

TABLE 16. Statistics of length (L), maximum width (W), width of hinge-line (HiW) and thickness (Th) of 15 pedicle valves of *Overtonia fimbriata* (J. de C. Sowerby).

TABLE 17

$\overline{L}$ mm. (var.) = 10·63 (3·272)
$\overline{W}$ mm. (var.) = 13·38 (5·338)
r = 0·945
a (var.) = 1·277 (0·0436)

$\overline{AdL}$ mm. (var.) = 1·82 (0·234)
$\overline{AdW}$ mm. (var.) = 3·47 (0·842)
r = 0·955
a (var.) = 0·600 (0·00793)

$\overline{L}$ mm. (var.) = 10·63 (3·272)
$\overline{AdL}$ mm. (var.) = 1·82 (0·234)
r = 0·975
a (var.) = 0·276 (0·00088)

$\overline{SpL}$ mm. (var.) = 3·63 (0·605)

TABLE 17. Statistics of length (L), width (W), length of adductor scars (AdL), width of adductor field (AdW) and length of the median septum (SpL) from the hinge-line of 6 brachial valves of *Overtonia fimbriata* (J. de C. Sowerby).

Genus ***AVONIA*** Thomas

1914 *Avonia* Thomas : 259.
1928 *Avonia* Thomas ; Muir-Wood : 36.
1960 *Avonia* Thomas ; Muir-Wood & Cooper : 185.

TYPE SPECIES. *Productus youngianus* Davidson 1860, by original designation of Thomas (1914 : 259).

DISCUSSION. The genus was briefly described by Thomas and emended by Muir-Wood, but not until 1960 was a full description of the genus available. One specimen figured as *Avonia youngiana* Muir-Wood & Cooper (1960, pl. 47, figs. 22–24) is not conspecific and should be referred to *Institifera tessellata* (de Koninck). The specimen, (BB.13593), has a deeper body cavity than *A. youngiana* ; a flatter brachial valve ; less elongate outline and more prominent and wider ribs. It agrees in all known respects with the specimen figured by Davidson (1861, pl. 33, fig. 25).

Interior features of the type species are poorly known and some of the species assigned to the genus by Muir-Wood & Cooper are doubtful. However, the original diagnosis of the genus stressed the characteristic external ornamentation which is spinose in the early stages but developed ribbing in late growth stages, towards the anterior margins. Davidson records that his species was abundant at Corrieburn, Stirlingshire (1860 : 181) and his figured specimen (1861, pl. 33, fig. 21) came from there. A single brachial valve interior, assigned to the species, is in the Davidson Collections (B.45681) and also came from Corrieburn. This brachial valve is closely comparable to specimens collected from Co. Fermanagh and attributed to *Avonia*.

The Irish shells display the distinctive ornamentation mentioned above, but differ from *A. youngiana* in attaining a larger size and in having a more rounded to transversely rectangular outline. Concentric lamellae are prominent and the specimens are probably conspecific with *Productus aculeatus* Sowerby.

A holotype does not appear to have been chosen for *A. youngiana*. A specimen from Corrieburn, in the Davidson Collection (B.45680), may well be the one upon which Davidson based his figures, both in 1860 (pl. 2, fig. 26) and in 1861 (pl. 33, fig. 21). It was figured by Muir-Wood (1928, pl. 12, figs. 9, 10) and is a complete shell showing the external ornamentation tolerably well. It should therefore, he considered as lectotype of *Avonia youngiana*.

There has always been some doubt regarding the validity of *A. youngiana* and *P. aculeatus*. Davidson discussed these species at some length (1863 : 233, 1880 : 311) but while retaining some doubts, he separated the two as distinct species. Thomas (1914) made *P. youngianus* the type species of *Avonia* and here *P. aculeatus* is included within that genus and designated as the type species of the new subgenus *Quasiavonia*. This is done only with the present system of Productoid classification in mind. It may prove more expedient in the future to consider many taxonomic groups as being more closely related than is now the practice. If so a greater use may be made of the subspecific status for forms that apparently differ only because of their environment. Such subspecies should converge morphologically in intermediate geographical or environmental regions.

Martin's specimen of *P. aculeatus* (BMNH. No. B.60992), used by Sowerby in 1814 for his description of the species, was chosen as lectotype by Muir-Wood (1951 : 101). Although this specimen is slightly abraded it is distinguishable from *A. youngiana*. by its more rounded outline, less well developed ribs and flatter brachial valve. However, the frequency of spines is more similar than was suggested by Davidson (1863), as can be seen from specimens of *A. Quasiavonia aculeata* from Settle, Yorkshire (B.5748), Dalry, Ayreshire (B.13940), and from the Fermanagh fauna (Pl. 11, figs. 3, 4).

Subgenus ***QUASIAVONIA*** nov.

DIAGNOSIS. Outline rounded quadrate to subcircular, prominent rounded ventral umbo, maximum width slightly greater than length, commonly at hinge-line; profile concavo-convex, about one-half as deep as wide, and with moderately deep body cavity; concentric lamellae more prominent on pedicle valve; spines suberect to recumbent, concentrically arranged and more or less radially aligned anteriorly, no true ribbing ; ventral adductor field indistinct, scars slightly raised, elongate ; dorsal adductor scars raised, elongately trigonal ; median septum low, extending beyond adductor scars.

Type species. *Productus aculeatus* Sowerby 1814.

Discussion. *Avonia* (*Quasiavonia*) *aculeata* is here considered as a distinct species group, having strong characteristics distinguishing it from *Avonia youngiana* but retaining several features, especially internally, which indicate a close relationship to that species. It is, therefore, assigned to the new subgenus *Quasiavonia*. *Quasiavonia* differs from *Overtonia* in being strongly lamellose on the pedicle valve, in the absence of prominent rugae, its finer spines and evenly concave brachial valve. The cardinalia are also distinct. *Krotovia* and *Levipustula* are not lamellose, have more densely arranged spines and less well defined dorsal adductor scars, while those of *Levipustula* are diamond-shaped (Muir-Wood & Cooper 1960, pl. 50, figs. 14, 15). The remaining genera, except *Avonia*, included within *Overtoniinae*, are all distinctive, and indeed, in some instances, bear little familial similarity e.g. *Rhytiophora* and *Stegacanthia*.

The new subgenus is included within *Avonia* because of similar dorsal interiors, similar transverse profiles, lamellose ornamentation and the tendency for *Quasiavonia* to show a slight ribbing on the flanks of adult valves. Differences are clear and sufficient to warrant supra-specific separation of the two. *Quasiavonia* reached a larger size than is known in well authenticated *Avonia* species ; its shape is more rounded, the width remaining about the same as the length throughout growth. In *Avonia*, beyond about 8 mm. long, the length increased relatively more than the width. A faint ribbing is restricted to the antero-lateral valve margins of adult *Quasiavonia* shells and the concentric ornamentation is perhaps more strongly lamellose. But the strength of development of " growth lines " and lamellae is of less importance than other features and is commonly difficult to assess because of differences in preservation. A delicate ornamentation of lamellae is more readily preserved in an etched silicified fauna, such as that described here, than on specimens broken from solid rock, from which both ornamentation and the external shell layers may be removed. For this reason the type specimen may appear less spinose and ornamented than it was in life.

As *Avonia youngiana* does not occur in the Fermanagh fauna it has not been possible to make a statistical comparison of the two species.

Avonia (Quasiavonia) aculeata (Sowerby)

(Pl. 10, figs. 8–17 ; Pl. 11, figs. 1–21 ; Text-fig. 10)

1809 *Conchyliolithus Anomites* (*aculeatus*) Martin : 8, pl. 37, figs. 9, 10.
1814 *Productus aculeatus* Sowerby : 156, pl. 68, fig. 4.
1914 *Pustula aculeatus* (Martin) Thomas : 320, pl. 19, figs. 9, 10, ?11.
(See also for earlier references.)
1951 *Productus* (?*Krotovia*) *aculeatus* (Sowerby) Muir-Wood : 101, pl. 3, fig. 3.

Diagnosis. Outline rounded quadrate to subcircular, width slightly greater than length, umbo rounded, extending beyond straight hinge-line, cardinal extremities commonly perpendicular and flattened, maximum width at or near hinge-line; profile concavo-convex, nearly one-half as deep as wide; young with epithyrid pedicle sheath; concentric lamellae strongly developed over pedicle valve, less prominent on brachial valves; recumbent to suberect spines of about equal diameter arise posterior to each concentric lamella, short spine bases anteriorly and irregular radial arrangement; growth lines distinguishable; brachial valve with fewer and finer tapering spines; incipient ribbing slightly developed on adult flanks of both valves; ventral muscle field indistinct, adductor scars elongately trigonal to lanceolate, separated by narrow depression; diductor scars probably more rounded, spreading on to umbonal slopes; spine openings retained anteriorly; flattened to concave articulatory surfaces along hinge-line with slight ridges bounding postero-lateral region of visceral disc; cardinal process small, sessile with lobes distinctly separated posteriorly, supported by lateral ridges diverging from hinge-line at about 25° and extending towards postero-lateral margins; adductor scars smooth, raised and elongately trigonal, extending about one-quarter valve length; median septum weak between adductor scars and extending about two-fifths valve length; brachial impressions indistinct, lobate, at about 45° from mid-line, extending from antero-lateral margins of adductor scars for about two-thirds valve length; surface finely tuberculate.

MEASUREMENTS (in mm.):

	length	width
Shell (BB.52859)	15·2	15·4
Brachial valve (BB.52861)	10·5	15·0
Shell (BB.52862)	12·5	15·0
Shell (BB.52863)	8·0	8·7
Pedicle valve showing pedicle sheath (BB.52866)	1·6	1·8
Incomplete brachial valve (BB.52864)	3·5	*c.* 3·8
Brachial valve (BB.52865)	*c.* 4·5	5·5

LOCALITIES AND HORIZON. Subreefal limestones and shales. Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. Spines and lamellae were formed at all stages of growth, and while the lamellae became somewhat more widely separated anteriorly, the spines retained approximately the same density by the addition of further spines to each concentric row. On pedicle valves more than 5 mm. long, the spine separation in each row is about 1 mm., varying to 2 mm. medianly. Each spine arose obliquely from the shell surface, with a slight spine-ridge behind it, and continued to grow at about 40° or less to the valve, except for a row flanking the anterior border of the "ears", which grow at a higher angle and somewhat postero-laterally. On the brachial valve the spines are commonly tapered and towards the cardinal extremities the spines curve medianly over the valve (Pl. 11, fig. 1). Juvenile pedicle valves 1·5 mm. long have a supra-apical pedicle sheath protruding posteriorly from an oval protegulal node about 0·2 mm. long. A shallow groove extends 0·4 mm. antero-ventrally from the protegulal node and is overhung by a pair of clasping spines 0·2 mm. apart (Pl. 11, figs. 9, 10). One further pair of clasping spines grew close to the hinge-line and about 1 mm. apart ; however, these were preceded by the first two pairs of ordinary oblique spines which formed the first spine row at a valve length of about 0·7 mm. Up to a length of 3 to 4 mm. the spines grew fairly symmetrically in pairs, with the rare addition of a median spine, but the number in any one concentric band did not exceed four. Beyond this length additional spines were added so that a distinct radial pattern was produced. The spines were evidently of considerable length as one pedicle valve, 4 mm. long, has a spine 5 mm. long still remaining in position.

The lamellae and growth-lines indicate that shell shape remained fairly constant during growth. The curvature of the pedicle valve is regular while that of the brachial valve is less marked and tends to be slightly flattened across the middle of the visceral disc. In specimens longer than about 8 mm., the lamellae bend laterally, near to the posterior margin, forming small ears at the cardinal extremities. However, more rapid growth anterior to this restricted the formation of acutely angled ears and maintained the greatest width at a point commonly just anterior of the hinge-line (Pl. 11, fig. 4).

In common with many Overtoniinae, the ventral interior is poorly developed. The adductor scars are elongately trigonal to lanceolate markings about two-fifths as wide as long, extending from the beak for about one-third of the valve's length. The strong curvature of the umbonal region apparently led to a continued migration of the adductor bases anteriorly, so that these muscles would have had a more direct pull to their dorsal areas of attachment. This migration prevented the development of strongly marked scars. The same was probably true of the diductor muscle scars, which are wider than the adductor scars and spread on to the umbonal slopes. The

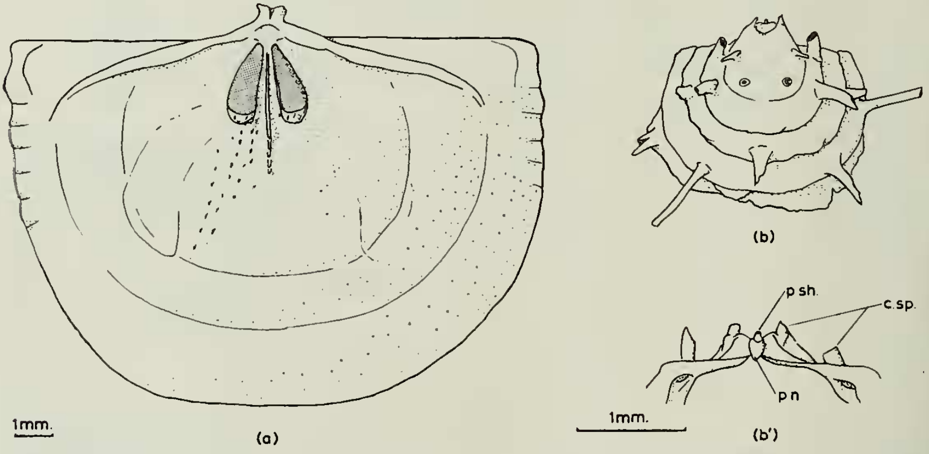

Fig. 10. Illustrations of the brachial valve interior (a), and a young pedicle valve viewed ventrally (b) and dorsally (b′) of *Avonia* (*Quasiavonia*) *aculeata* (J. Sowerby) *p.sh*, pedicle sheath ; *c.sp*, clasping spine bases ; *p.n*, protegulal node of the pedicle valve.

cardinal process of young valves, up to about 5 mm. long, is distinctly bilobed, the two lobes remaining separated by a deep groove posteriorly, but beyond this length the groove became less distinct and although the divergence of the myophores continued, at about 35°, secondary shell filled most of the intervening space. At the same time the lateral ridges grew posteriorly along the flanks of the cardinal process so that in the adult shell they extend well beyond the hinge-line (Pl. 10, fig. 13) The posterior margins of these ridges evidently articulated against the flattened to concave areas along the ventral hinge-line, which are anteriorly enclosed by slight ridges diverging across the inner margins of the ears from just inside the ventral umbo (Pl. 11, fig. 8).

The dorsal adductor scars are commonly distinguishable in valves 3 mm. long and extend for 1 mm. in length and slightly less in width. However, during growth their length, proportional to that of the valve, decreased, so that in valves about 10 mm. long the adductor scars are only one-quarter of this length (Pl. 11, fig. 16). At the same time the width of the adductor field grew to be rather greater than its length. Although the scars are well separated medianly, the median septum did not begin to form until valves were at least 5 mm. long. Thereafter its growth remained constant at about two-fifths of the valve length.

Several shells, both pedicle and brachial valves, have holes bored of about 0·5 mm. in diameter and these are thought to have been made by carnivorous gastropods.

TABLE 18

$\overline{L}$ mm. (var.) = 5·70 (15·499)
$\overline{W}$ mm. (var.) = 6·10 (19·637)
r = 0·987
a (var.) = 1·128 (0·00173)

$\overline{L}$ mm. (var.) = 5·70 (15·499)
$\overline{Th}$ mm. (var.) = 2·70 (4·677)
r = 0·895
a (var.) = 0·549 (0·00316)

TABLE 18. Statistics of length (L), maximum width (W) and thickness (Th) of 21 pedicle valves of A. (*Quasiavonia*) *aculeata* (*Sowerby*).

Genus ***KROTOVIA*** Fredericks 1928

1928 *Krotovia* Fredericks : 779, 790.
1952 *Krotovia* Fredericks ; Sarycheva & Sokolskaja : 92.
1960 *Krotovia* Fredericks ; Muir-Wood & Cooper : 188.

EMENDED DIAGNOSIS. Subcircular, width commonly slightly greater than length, hinge-line straight, more than one-half maximum width, venter rounded umbo prominent and extending beyond hinge-line ; strongly concavo-convex, about one-half as deep as long, body cavity narrow ; concentric ornamentation of growth lines and rare poorly developed lamellae ; fine suberect spines from small rounded tubercles with variably developed quincuncial arrangement ; umbonal slopes and cardinal extremities with weak irregular rugation ; brachial valve similar but also dimpled ; ventral adductor scars elongately trigonal, diductor scars elongately pear-shaped, extending beyond adductor scars on to umbonal slopes ; spines commonly retaining internal openings ; cardinal process small, sessile, lobes well separated posteriorly and narrowly incised ; lateral ridges supporting process, extending posteriorly of hinge-line and anteriorly diverging from it at 20° to 30° towards postero-lateral margins, rarely extended as marginal ridge ; adductor scars ill-defined, elongately trigonal, postero-ventrally directed ; median septum poorly developed, about one-third valve length ; tuberculate.

Type species. *Productus spinulosus* J. Sowerby 1814, by original designation of Fredericks (1928).

Discussion. The genus was briefly defined by Frederick (1928) and redescribed by Muir-Wood & Cooper (1960 : 188), but as the internal characteristics of the type species, *P. spinulosus*, were then unrecorded, their description of the interiors was based upon *P. wallacianus* Derby, from the Lower Pennsylvanian of Brazil. The genus has much in common with *Avonia*, the new subgenus *Quasiavonia*, *Overtonia* and *Levipustula* of the Overtoniinae Muir-Wood & Cooper. It is distinguished from them by its lack of a differentiated concentric ornament in the form of rugae, strong lamellae or grouped and banded spines, and from *Levipustula*, in particular, in not having elongate spine bases, its weaker median septum and differently shaped adductor scars (cf. *Levipustula* Muir-Wood & Cooper 1960, pl. 50, fig. 15). The dorsal muscle scars of *Krotovia* are commonly less well developed than those of other genera within the subfamily.

Although commonly described as having a smooth surface, this is not entirely true, for apart from the development of incipient rugation towards the posterior margins of both valves, growth lines are occasionally accentuated as subdued lamellae.

Each spine is swollen at its base, so that shells from which the spines have been broken are ornamented by low rounded tubercles. These may be worn from abraded shells leaving a characteristic pattern of holes. The spines themselves are at a high angle to the shell, commonly at about 80°, delicate and all of much the same size. The quincuncial pattern is commonly best developed posteriorly, the spines anteromedianly being more widely spaced and less regular. Towards the adult anterior margin the spines tend to form more regular, closely arranged concentric rows.

Krotovia spinulosa (J. Sowerby)

(Pl. 12, figs. 1–18 ; Pl. 13, figs. 1–7)

1814 *Productus spinulosus* J. Sowerby : 155, pl. 68, fig. 3.
1861 *Productus spinulosus* J. Sowerby ; Davidson : 175, pl. 34, figs. 18–21.
1914 *Pustula spinulosa* (J. Sowerby) Thomas : 314, pl. 18, figs. 7–9, pl. 19, fig. 7, *non* fig. 8.
1928 *Krotovia spinulosa* (J. Sowerby) Fredericks : 779, 790.
1952 *Krotovia spinulosa* (J. Sowerby) ; Sarycheva & Sokolskaja : 92, pl. 14, fig. 98.

Emended diagnosis. Outline subcircular, width slightly greater than length, hinge-line about five-sixths maximum width, cardinal extremities commonly perpendicular ; profile strongly concavo-convex, nearly one-half as deep as long ; shell surfaces more or less smooth with sporadic development of lamellae and distinct growth lines ; spines uniform in size, fine suberect at about 80° to surface, arising from quincuncially arranged low tubercles, about four in width of 2·5 mm., 5 mm. antero-medianly from ventral umbo ; umbonal slopes and cardinal extremities with incipient rugation ; adult anterior venter vaguely ribbed ; brachial valve similar but dimpled surface ; ventral adductor field about one-fifth valve length, anteriorly directed ; diductor scars extending beyond adductor scars, poorly defined ; cardinal process lobes deeply but narrowly incised dorsally, internally with pair of nodes at lobe bases, anterior to which strong lateral ridges cross and diverge from hinge-line at about 30° ; lateral ridges commonly terminating towards postero-lateral margins, rarely continued as circumvisceral ridge ; adductor scars commonly invisible, elongately trigonal, slightly raised and about one-fifth valve length ; median septum rarely developed, thread-like and about one-third valve length ; surface finely tuberculate, brachial markings indistinguishable.

MEASUREMENTS (in mm.) :

	length	width
Complete shell (BB.52867)	13·7	14·9
Complete shell (BB.52868)	6·8	7·5
Pedicle valve (BB.52869)	7·0	—
Pedicle valve (BB.52870)	4·4	4·1
Brachial valve (BB.52871)	7·8	9·6
Incomplete brachial valve (BB.52875)	6·0	*c.* 7·4
Complete brachial valve (BB.52874)	1·4	1·5
Complete shell (BB.52876)	14·8	16·0

LOCALITIES AND HORIZON. Subreefal limestones and shales, Bunnahone and Carrick Loughs, 2 miles N.W. of Derrygonnelly, Co. Fermanagh, and Dockra limestone (BB.52876–77), Cunningham Baidland, Ayrshire, D_1.

Krotovia lamellosa sp.n.

(Pls. 13, figs. 8–16 ; Pl. 14, figs. 1–19)

DIAGNOSIS. Subcircular, concavo-convex *Krotovia* of same shape as type species ; concentric ornamentation of growth lines, well developed lamellae and spine rows, spines suberect to recumbent anteriorly, slight quincuncial pattern and spines of different sizes within each interlamellose band ; internally like type species, but perhaps more distinctly developed adductor scars and median septum.

MEASUREMENTS (in mm.) :

	length	width
HOLOTYPE. Complete shell (BB.52878)	9·0	10·1

		length	width
PARATYPES.	Complete pedicle valve (BB.52879)	9·1	9·6
	Incomplete pedicle valve showing ornament (BB.52880)	7·6	8·1
	Incomplete pedicle valve (BB.52881)	7·5	—
	Incomplete young pedicle valve (BB.52888)	2·1	—
	Complete pedicle valve (BB.52889)	1·8	1·9
	Complete brachial valve (BB.52883)	5·7	7·0
	Incomplete brachial valve (BB.52884)	7·3	—
	Complete brachial valve (BB.52885)	4·2	4·6
	Complete brachial valve (BB.52886)	4·1	4·6
	Incomplete brachial valve (BB.52887)	3·1	—

DISCUSSION. The external form and characteristics of *K. spinulosa* were re-described in detail by Thomas (1914 : 314), and from this, and other works, there seems little doubt that the present material is conspecific, and of use, therefore, in the emendation of both the genus *Krotovia* and the type species itself. Previously the internal characteristics of *K. spinulosa* were unrecorded, and while those of the present material are poorly impressed, they do, nevertheless, generally accord with those described for *Productus wallacianus* Derby by Muir-Wood & Cooper (1960 : 188). Although dorsal valves of the size (about 15 mm.) illustrated by these authors (pl. 50, fig. 11) are not available, it does seem that the cardinalia were less well developed than in *P. wallacianus*. However, despite their description of the dorsal adductor scars being " elongate subquadrate in outline ", the plate figure shows them to be the same shape as those of *K. spinulosa* i.e. elongately trigonal. The cardinal process is described as having a " minute median lobe posteriorly developed ", such a structure is not present in *K. spinulosa*. The two lobes of the cardinal process diverged at about 40° from one another throughout their development, as seen dorso-posteriorly, and retained a distinct cleft distally. Each lobe was deeply incised for the reception of the diductor muscles, and their enclosing ridges occasionally grew to such an extent as almost to surround the muscle bases. As growth proceeded the median pair of ridges, bordering the muscle bases, grew closer together at their proximal end, i.e. at the exterior base of the cardinal process, so that in adult valves these ridges are adjacent for one-half their length, before curving outwards to the distal tips of the lobes (Pl. 12, fig. 17). It could be that in poorly preserved material this basal region, where the median ridges are adjacent, may simulate a solid secondarily developed ridge. The primary positions of the tips of the lobes are commonly marked, in older valves, by a pair of nodes on the basal, ventral surface of the cardinal process (Pl. 12, fig. 18), growth having been by the addition of shell laterally and dorso-posteriorly.

The lateral ridges were strongly developed throughout growth, being distinguishable in brachial valves about 1 mm. long. In valves about 5 mm. long, their median ends had extended beyond the hinge-line, along the lateral flanks of the cardinal process, while their lateral extremities commonly merged into one of the poorly defined concentric rows of internal tubercles. The valve length at which the adductor scars developed is very variable, but they can be seen rarely at this stage of growth (Pl. 12, fig. 13).

The spines are more or less regularly spaced over the two valves. Each spine has a rather swollen base, and these show as rounded tubercles in shells from which the spines have been broken. Towards the anterior margin of adult pedicle valves, more than 12 mm. long, the spine bases are somewhat elongate and contribute to a faint and irregular " ribbing ". This resembles *Overtonia* in that the incipient rib commonly continues anteriorly only to a point between the pair of anteriorly placed spines and then is lost. The spines are directed at a high angle from the valves but tend to curve ventrally, so that those placed on the lateral flanks of the pedicle valve may be at only about 40° to the surface. On the brachial valve the spines towards the postero-lateral margins curve antero-medianly.

The characteristic quincuncial pattern of spines on *K. spinulosa* is best developed over the posterior part of the shell, particularly within the first 7 to 8 mm. It is commonly lost antero-medianly because of a wider spacing of the spines in this region. However, some specimens, with particularly smooth surfaces, retain the regular pattern throughout a length of 15 mm. The occasional development of a lamella disrupts the pattern and commonly is followed by a rather more closely spaced concentric row of spines, having a modal value of 5 spines in 2·5 mm. width. Table 20 (A) gives the spine distribution. The tendency towards irregularity of this spine pattern is more marked in specimens from Co. Fermanagh than some collected from the Dockra limestone of Aryshire, and these latter shells have less frequently developed incipient lamellae.

The fauna from Co. Fermanagh contains approximately equal numbers of specimens of *K. spinulosa* and *Krotovia lamellosa* sp. nov. The taxonomic position of the latter is uncertain, and they may be merely lamellose varieties of *K. spinulosa*. The shells of *Krotovia lamellosa* are of the same shape as those of *K. spinulosa*, there being no significant difference between their lengths as compared to maximum widths or thickness ($P > 0{\cdot}5$). The only distinction made, at present, is in the form of the external ornamentation ; that of *Krotovia lamellosa* being clearly lamellose and with spines more obviously concentrically arranged. The spines do not have the same basal swellings as those of *K. spinulosa*, and are not all of the same diameter, although there is an indistinct quincuncial pattern.

The frequencies of the spines in the two species are set out in Table 20. Pedicle valves more than 5 mm. long commonly lose the quincuncial pattern and between the lamellae the spines are arranged in irregular bands with those more anteriorly placed having a slightly smaller diameter and placed radially between the posterior ones. In this way the interlamellose bands may have up to three ranks of spines, and this in itself gives a local diagonal pattern (Pl. 13, fig. 11). This is reminiscent of the arrangement on members of the Echinoconchinae, but those shells contrast with the present material in having almost flat brachial valves and different interiors. The grouping of spines into interlamellose bands is only sporadically developed and probably the two features are linked, in other words the formation of a lamella inhibited spine growth for a short period, after which the spines were more crowded than usual until the formation of the next lamella. Indeed, it could be argued that *Krotovia lamellosa* is *K. spinulosa* in which lamellae have been more strongly developed than is usual. However, gradational forms are not found in the fauna so the external differences are considered to be valid specific characteristics, and there is a tendency for the lateral ridges to be less divergent and the dorsal adductor scars better developed in *K. lamellosa* than in *K. spinulosa*.

Despite the ventral beaks commonly having been broken in these shells, it is possible to collect material showing a minute pedicle sheath, about 0·03 mm. in diameter, ventral to which is the usual shallow groove. In common with other juvenile productoid shells, there are usually two pairs of clasping spines that curve posteriorly over the beak and probably assisted in the attachment of the young shells.

TABLE 19

	A	B
$\bar{L}$ mm. (var. L.)	7·07 (13·246)	5·94 (4·998)
$\overline{Th}$. mm. (var. Th.)	3·28 (4·120)	2·89 (1·529)
r	0·989	0·988
$\log_e \bar{L}$ (var. $\log_e$ L)	1·837 (0·2382)	1·716 (0·1328)
$\log_e \overline{Th}$ (var. $\log_e$ Th)	1·024 (0·3243)	0·893 (0·1681)
r_e	0·995	0·996
α (var. α)	1·666 (0·00005)	1·2335 (0·0005)

TABLE 19. Statistics of length (L) and thickness (Th) of 30 shells and pedicle valves of *Krotovia spinulosa* (J. Sowerby) (A), and 21 shells and pedicle valves of *Krotovia lamellosa* sp. n. (B).

TABLE 20

	A				B		
No. of spines	3	4	5	6	4	5	6
At 5 mm.	1	14	9	1	5	10	5
At 10 mm.	4	3	0	0	0	0	0

TABLE 20. The number of spines counted in a width of 2·5 mm. at a distance of 5 mm. and 10 mm. antero-medianly from the ventral umbo of *Krotovia spinulosa* (J. Sowerby) (A), and *Krotovia lamellosa* sp. n. (B).

Family **MARGINIFERIDAE** Stehli 1954

Subfamily **MARGINIFERINAE** Stehli 1954

Genus ***EOMARGINIFERA*** Muir-Wood 1930 : 103

Type species. *Productus longispinus* J. Sowerby, by original designation of Muir-Wood (1930 : 103).

Discussion. *Eomarginifera* was erected in 1930 to include small quadrate shells with ribs developed throughout life ; six symmetrically arranged spines on the pedicle valve ; lamellose thickenings around the brachial valve margins and with poorly developed internal marginal ridges. In addition to the type species, Muir-Wood included *Productus derbiensis* Muir-Wood, *P. lobatus* J. Sowerby, *P. minutus* Muir-Wood, *P. praecursor* Muir-Wood, *P. pseudoplicatilis* Muir-Wood, *P. setosus* Phillips, *P. tissingtonensis* Sibly and *P. triquetrus* Muir-Wood, in *Eomarginifera*. Of these forms *P. minutus* and *P. triquetrus* have since been tentatively assigned to *Alifera* by Muir-Wood & Cooper (1960). These authors did not assign *P. pseudoplicatilis*, which has here been included in *Plicatifera* (see p. 204). *P. tissingtonensis* was also left unplaced, although it is referred to *Eomarginifera* in the text (1960 : 220).

There is a proliferation of species within *Eomarginifera* and related genera, showing considerable variation and the complete group warrants a thorough reinvestigation. Unfortunately, such a study is beyond the scope of the present work. Meanwhile all that can be said is that specimens at present assigned to *Alifera panderi* (= *P. minutus*) include some belonging to the new subgenus *Eomarginiferina* (e.g. some specimens in the British Museum (Natural History) from Little Island, Cork and from Derbyshire), and that *Eomarginifera* Muir-Wood 1930 appears to include large coarsely ribbed forms like *E. lobata* and smaller shells with either wide or narrow ribbing, such as *A. panderi* and *E. longispina* respectively. The presence or absence of major spines on the hinge-line may prove to be of diagnostic value. Such spines are never found on the newly described Fermanagh valves.

By including *Eomarginiferina* as a new subgenus of *Eomarginifera* it is necessary to emend the generic description given by Muir-Wood & Cooper (1960 : 209) with regard to the spines and the pedicle valve interior. The pedicle valve ornamentation must include : juvenile spines or spine-bases posteriorly confined, major spines symmetrically arranged, commonly in threes, near cardinal extremities, on umbonal slopes and on anterior venter. Interior of pedicle valve commonly traversed by prominent ridges corresponding to rib interspaces and extending to trail, lobate diductor scars enclosing elongate-oval adductor scars posteriorly confined ; marginal ridge rarely developed.

Subgenus ***EOMARGINIFERINA*** nov.

1930 *Eomarginifera* Muir-Wood : 103 (pars).
1960 *Alifera* Muir-Wood & Cooper : 207 (pars).

Diagnosis. Outline subrounded with flattened triangular ears at greatest width of shell, adult anterior margin commonly extended by low fold; profile subhemispherical, concavo-convex, bachial valve gently concave across visceral disc but strongly curved anteriorly forming short trail, body cavity moderately deep; radial ornament of low rounded costae, with rare bifurcations, forming reticulate pattern over visceral regions through intersection with rounded persistent rugae; spines confined to pedicle valve, three strong cylindrical spines, one pair laterally directed from each umbonal slope, single median spine slightly anterior of rugate region; young with pedicle sheath, clasping spines and small spines arranged on rugae umbonally; internally ventral visceral region traversed by strong ridges corresponding to rib interspaces and with additions by intercalation corresponding to external bifurcations, ridges posteriorly flattened by flabellate diductor field, anteriorly irregularly spinose; ears strongly demarcated by ridges curving from near hinge-line; three principal spines retain internal openings and rimmed by secondary shell; cardinal process squat, lobes separated internally by shallow groove, fused posteriorly, supported by lateral ridges that diverge from hinge-line and continue round inside of ears as strong ridges, commonly dying out around antero-lateral margins; adductor scars smooth, divisible into raised subtrigonal anterior scars and irregular oval posterior scars; low thickened ridge connects base of cardinal process to anterior adductor scars; median septum low between scars, narrow but high anteriorly, extending to about mid-length of valve; brachial ridges lobate to reniform with antero-lateral raised areas; strong anteriorly directed tubercles on anterior region of disc, finely tuberculate elsewhere.

TYPE SPECIES. *Eomarginifera* (*Eomarginiferina*) *trispina* subgen. et sp. n.

DISCUSSION. The subgenus is typically marginiferid in its small size, rather globose profile and few symmetrically arranged spines. But it does not agree in the marginiferinid characteristic of having a " brachial interior with a marginal ridge bounding the visceral disc " (Stehli 1954 : 321). In this respect the genus is reminiscent of the Costispiniferae, members of which have " crenulated ridges extending across the ears of both valves; prominent endospines in row anterior of septum " (Muir-Wood & Cooper 1960 : 217). However, in other characteristics the genus is quite unlike those included under the Costispiniferae but similar to those of the Marginiferinae, the subfamily under which *Eomarginiferina* is here assigned. Because of this anomaly it is desirable to redefine these subfamilies and the following emended diagnoses are suggested: Marginiferinae. Marginiferidae commonly with continuous externally crenulated, marginal or submarginal ridges around viceral disc of brachial valve externally free of spines. Costispiniferinae: Marginiferidae with crenulated ridges across ears of both valves; prominent endospines anterior to brachial impressions and both valves typically externally spinose. The genera included by Muir-Wood & Cooper (1960 : 205) within the Marginiferinae, with the exception of some *Eomarginifera* species, commonly have an antero-ventral sulcus. Two-thirds of the adult specimens of *Eomarginiferina* have a low antero-median fold; no specimens are sulcate. There is a consistent development of three strong spines, arranged symmetrically at about the same growth stage in a manner quite unlike other described genera. Certain specimens of *Alifera panderi* Muir-Wood & Cooper 1960 have three spines similarly arranged, and although described as having " six major spine bases " (Muir-Wood 1928 : 195) they may prove to be congeneric, if not conspecific with *Eomarginiferina trispina*.

The morphology of the subgenus is most closely related to *Eomarginifera* and *Alifera*. It differs from the former in its folded anterior margin, spine arrangement, smaller adult size and different dorsal adductor scars. *Eomarginiferina* differs from *Alifera* in not being anteriorly sulcate ; in having fewer rugae ; a different spine arrangement ; in its lack of a ventral marginal rim, and in its dorsal interior. It appears from pl. 66, figs. 13 and 17 (Muir-Wood & Cooper 1960) that the ventral interiors may have been similarly ridged and spinose (cf. Pl. 16, fig. 18).

The ventral interior of *Eomarginifera* is described by Muir-Wood & Cooper as having " flabellate diductor scars " that extend " to the end of the visceral disc ". It is unlikely, however, that the diductor scars could have extended to the anterior margin of the visceral disc of this genus and still have left room for the important brachial cavity. The brachial scars of the genus are suggestive of a well formed lophophore hanging into an open brachial cavity. Pedicle valve interiors of type material of *Eomarginifera* are poorly represented, but it is suggested that the diductor scars of Muir-Wood & Cooper may be the prominent ridges of *Eomarginiferina*, which are fully described under *E. trispina*. It is relevant to note that etched specimens of eomarginiferids studied by the author and collected from linestones of D. age from Cunningham Baidland, Ayrshire, do possess similar ridges to those of *Eomarginiferina*, and also show well developed posteriorly placed adductor and diductor scars.

Until such time as a full revision of *Eomarginifera* and related genera is undertaken, *Eomarginiferina* is retained as a subgenus, but some species presently ascribed to *Eomarginifera* or *Alifera* may well belong within this species group, and necessitate its elevation to generic rank.

Eomarginifera **(*****Eomarginifera*****)** ***trispina*** subgen. et sp.n.

(Pls. 15, figs. 9–22 ; Pl. 16, figs. 1–22 ; Text-fig. 11)

?1928 *Productus minutus* Muir-Wood : 195, (pars), *non* pl. 12, fig. 3.

DIAGNOSIS. Outline subrounded, greatest width at or equal to straight hinge-line, length about five-sixths maximum width, ears commonly prominent and demarcated from umbonal slopes by shallow groove ; profile subhemispherical with slight geniculation at deepest part of valve, greatest thickness about two-thirds length ; body cavity about two-ninths shell length ; short antero-dorsally directed trail, commonly with slight median fold ; multicostellate, ribs low, rounded and persistent, six in 2·5 mm. at 5 mm. antero-medianly of ventral umbo ; nine or ten rugae, commonly persistent, rounded and increasing in width anteriorly ; pedicle valve sparsely spinose, typically with three strong erect spines arising symmetrically and nearly concentrically, pair on umbonal slopes projecting laterally beyond cardinal extremities and single one projecting antero-ventrally from mid-valve, anterior of rugation ; small sub-erect spines on first 3 mm. from umbo, arising from intersections of costae and rugae ; ventral interior traversed by strong spinose ridges corresponding to intercostal spaces, spinose nature prominent anteriorly, ridges flattened and indistinct posteriorly, in region of indistinct small median adductor scars and flabellate diductor scars ; ears strongly demarcated ; cardinal process with short shaft, lobes internally divergent and separated by shallow groove, myophores posteriorly directed ; lateral ridges diverge from hinge-line at about 20° for about two-thirds hinge width, continue around insides of ears as strong externally crenulated ridges ; adductor scars smooth, anterior scars raised, subtrigonal, posterior scars irregularly rectangular, both surrounded by secondary shell in adult valves, about one-quarter valve length ; median septum narrow, low between adductor scars and posteriorly buried in secondary shell forming low broad, medianly grooved ridge to base of cardinal process ; septum high anteriorly and extending about one-half valve length ; postero-lateral brachial ridges from near junctions of anterior and posterior adductor scars, at about 60° to mid-line, extending about five-eighths valve length and forming lobate to reniform impressions enclosing thickened areas antero-laterally ; anteriorly directed spine-like tubercles irregularly arranged radially and concentrically.

MEASUREMENTS	(in mm.) :	length	width
HOLOTYPE :	Complete shell (BB.52890)	8·2	c. 10·4
PARATYPES :	Complete shell (BB.52891)	9·0	8·5
	Complete pedicle valve (BB.52892)	9·0	8·3
	Pedicle valve (BB.52893)	9·5	10·7
	Pedicle valve (BB.52894)	9·5	8·5
	Incomplete shell (BB.52903)	c. 9·0	11·8
	Brachial valve (BB.52895)	8·0	10·0
	Brachial valve (BB.52896)	5·0	7·5
	Brachial valve (BB.52897)	7·0	6·8
	Incomplete pedicle valve, to show spine pattern (BB.52898)	6·7	9·2
	Incomplete shell with juvenile spines (BB.52899)	6·5	8·3
	Juvenile pedicle valve showing pedicle sheath (BB.52900)	3·2	3·6

LOCALITIES AND HORIZON. Subreefal argillaceous limestones of Carrick and Bunnahone Loughs, and rarely in reef breccias of Knockmore, near Derrygonnelly, Co. Fermanagh. D_1.

DISCUSSION. The species is characterized by its small size, three symmetrically placed major spines and common development of a slight fold in the trail of adult pedicle valves. This fold is associated with a shallow V-shaped extension to the median part of the trail, although the brachial valve remains unfolded.

The two lateral spines are placed below the ears, close to their junctions with the umbonal slopes, and extend more or less laterally. They are set about five-sixths of the body width from each other and on the anterior ruga. The median spine is placed at about three-fifths of the valve length, measured from the hinge-line, a little anterior of the anterior ruga, commonly on one of the radial ribs, and is antero-ventrally directed. The growth of these three spines occurred at a similar stage of development, and one at which the brachial valve curved strongly against the pedicle valve to form the trail. Prior to this, the strong curvature in the growth of the pedicle valve must have caused the anterior commissure to rotate antero-dorsally relative to the surface of the substratum. It is postulated, therefore, that the small spines scattered over the first 2 to 3 mm. of the pedicle valve helped to anchor the young shell, while at adulthood, when the relative rotation of the brachial valve had ceased, the three major spines grew and in so doing helped to maintain the position of the shell. In 5 out of about 200 pedicle valves the median spine is replaced by two closely, but irregularly, situated spines. Such valves are considered as freaks and the duplication may have resulted from damage. On the other hand it could be a sign of the tendency for the growth of additional spines, seen more fully developed in the previously established genera of the Marginiferidae.

The adult radial ornament is distinguishable over the complete shell. Bifurcations of the costae are rare, but several commonly occur at the same growth stage. The costation is more persistent than the rugation and 5, 15, and 8 valves have 5, 6 and 7 ribs in 2·5 mm., 5 mm. antero-medianly of the ventral umbo. The ribbing is less clearly distinguishable on young shells and posteriorly.

The strong radial ridges inside the pedicle valve occur along the interspaces of the

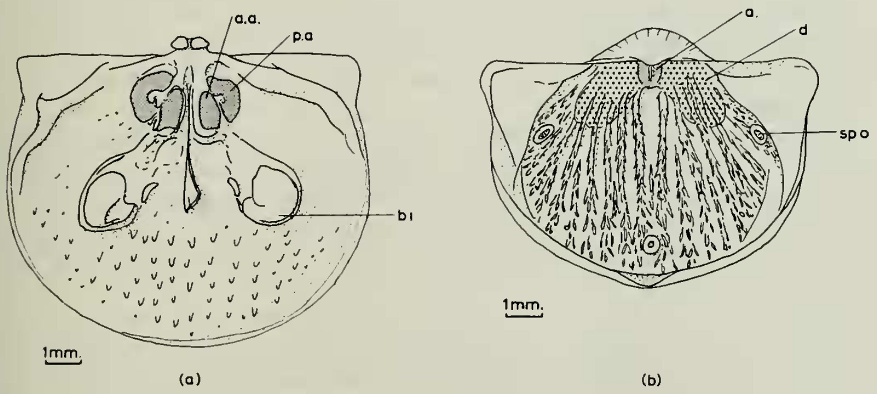

FIG. 11. Illustrations of (a) the brachial valve interior and (b) the pedicle valve interior of *Eomarginifera* (*Eomarginiferina*) *trispina* sp. n. to show the internal morphology; *a.a*, anterior adductor scars; *p.a*, posterior adductor scars; *b.i*, brachial impressions; *a*, adductor scars; *d*, diductor scars; *sp.o*, spine opening.

costellation, so that a bifurcation of a rib is represented internally by the intercalation of an additional ridge. The ventral interior is almost smooth posteriorly, except for a slight median ridge which probably separated the adductor scars (Text-fig. 11, b). The strong radial ridges extend anteriorly from the smooth region over the complete visceral surface, to the point where the brachial valve geniculated against the pedicle valve, i.e. to about the position of the opening of the single antero-median spine. Towards their anterior ends the ridges become increasingly tangled by a complex of more or less anteriorly directed spinose tubercles (Pl. 16, fig. 18). However, the connections to the lateral spines, and commonly to that of the antero-median spine remained open allowing the continued life of those spines, even after the development of the tuberculate ridges had surrounded them (Pl. 16, fig. 22). A study of a growth series of ventral interiors reveals that these ridges only developed when the shell had almost fully grown, and they became increasingly prominent with age. The development of the spinose tubercles on the ridges anteriorly was followed by the break down of the ridges themselves leaving only the spinose mass over the anterior one-half of the visceral region. At the same time flattening and resorption of these ridges occurred posteriorly producing flabellate areas considered to be the diductor scars, which extended about 3 mm. from the beak. The intimate relationship between internal and external ribbing, together with its extension over the complete visceral interior, precludes the possibility that these ridges were the attachment areas for the diductor muscles. Their position and development suggests that they were formed as a result of an extensive and closely pinnate mantle canal system, and in all probability represent the ridges between the gonocoel canals. Hence their late development, at sexual maturity, followed by the anterior break down of the ridges as the gonadal strands increased in size, and the tubercles which retained the mantle muscle strands which assisted in the circulation and expulsion of the gonadal products. The rudimentary mantle canals were outward folds of the mantle and these controlled the external radial ornament. A dichotomy of the mantle canal occurred during the bifurcation of the rib, while internally shell deposition between the canals produced the ridges and intercalations between the canal branches.

A closely comparable development of ridges between the gonocoels of *Alifera konincki* Muir-Wood & Cooper are illustrated by these authors (1960, pl. 66, figs. 6, 8, 13, 16, 17) on internal moulds, but are not mentioned in the text where the " subflabellate diductor scars " are mistakenly described as " not enclosing adductor scars " (: 207). The dorsal interiors and form of the shells clearly distinguish these two species.

Spats of *E. trispina* were probably attached during their early development by a pedicle which extruded through a small posteriorly directed pedicle sheath (Pl. 16, figs. 3, 4). In common with several other productacean genera, the brephic valve was shallowly grooved, perhaps through some bipartite development inherited from the larval stage, and was probably furnished with a pair of small encircling spines. Besides these spines, two pairs of clasping spines developed close to the hinge-line and about 1 mm. and 1·75 mm. apart. These spines curved ventro-posteriorly in such a way as to have gripped any suitably placed object, and rarely were incurved to make contact with their own valve surface after which they continued to grow along the surface for some distance (Pl. 15, fig. 9). This behaviour indicates the way in which the growing spine must have been capable of altering its direction of growth, in response to solid objects, by the varied proliferation of columnar epithelium at the tip of the spine mantle tissue (Williams 1956 : 252). Fourteen to sixteen additional fine, suberect spines developed from the rugae in more or less symmetrical pairs, together with one or two medianly placed spines, over the first 2 or 3 mm. of the pedicle valve. No more spines were produced until the three major spines developed after a further growth of between 4 and 6 mm. (Text-fig. 4 a–c).

Ribbing and growth-lines are the sole ornamentation anterior of the median major spine. The rib immediately anterior of this spine may continue rather broader than the others, and along the trail forms the crest of the shallow median fold. This fold was seen in 34 out of 45 valves, and is rather variable in its form. Commonly from 1 to 3 mm. of the antero-dorsal margin of the pedicle valve are folded into a shallow V, but rarely the fold is less pronounced while the whole margin is extended more anteriorly than usual. A slight, but apparently similar fold is seen on *Eomarginifera praecursor* (Muir-Wood). The external form and costellation also seem similar, but the species differ in that *E. praecursor* has six major spines on the pedicle valve (Muir-Wood 1928 : 192). Unfortunately it has not been possible to compare internal characteristics.

Because of the high proportion of articulated shells, and the delicate nature of young brachial valves, it has not been possible to trace the development of the brachial valve throughout its growth. It is clear, however, that while the anterior adductor scars were slightly raised and clearly distinguishable for much of the shell's growth, the posterior adductor scars only became clearly differentiated in adulthood, by the development of surrounding secondary shell, and probably only after the trail had formed. The median septum was developed anteriorly, from between the adductor scars, and was always highest anteriorly. The low broad ridge from the base of the adult cardinal process and median ends of the lateral ridges which connect to the posterior ends of the anterior adductor scars, is made of secondary shell substance and developed at about the same time as the thickening around the posterior scars and the platforms within the brachial impressions. This posterior median ridge bifurcates close to the cardinal process with the formation of a shallow groove leading down to the depression between the anterior adductor scars, from which the median septum arises. The brachial impressions are distinguishable in valves with a visceral disc about 5 mm. long. But not until reaching a visceral length of about 6 mm. did the antero-lateral regions become strongly thickened. The lateral ridges were probably distinguishable medianly from an early stage, and the ridges demarcating the ears (" ear-baffles ") were certainly present when the valve was 5 mm. long. It was not until growth had continued beyond this length that the lateral ridges merged with the ear baffles as a continuous line of shell thickening. This pattern of growth is common to several productacean genera, e.g. *Plicatifera* and *Overtonia* (Text-fig. 5).

TABLE 21

$\overline{L}$ mm. (var.) = 7·46 (0·367)
$\overline{W}$ mm. (var.) = 8·72 (0·144)
$\overline{SpL}$ mm. (var.) = 4·53 (0·313)
$\overline{SpW}$ mm. (var.) = 7·18 (0·203)

TABLE 21. Statistics of length (L.), width (W), the distance from the umbo to the median major spine (Sp L), and the distance between the lateral pair of spines (SpW) of 20 adult pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

TABLE 22

No. of rugae	8	9	10	11	12
No. of specimens	1	9	6	5	2

TABLE 22. The number of rugae counted across the visceral region of 23 pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

TABLE 23

No. of ribs	5		6		7
No. of specimens	5	2	15	0	8

TABLE 23. The number of radial ribs counted in 2·5 mm. at a distance of 5 mm. antero-medianly from the umbo of 30 pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

TABLE 24

$\overline{L}$ mm. (var.) = 6·00 (4·096)
$\overline{Th}$ mm. (var.) = 2·49 (1·949)
r = 0·961
Log$_e$ $\overline{L}$ (var. log$_e$ L) = 1·738 (0·108)
Log$_e$ $\overline{Th}$ (var. log$_e$ Th) = 0·775 (0·274)
r_e = 0·972
α (var.) = 0·5037 (0·000496)

$\overline{L}$ r mm. (var.) = 4·90 (1·481)
$\overline{Th}$r mm. (var.) = 1·25 (0·181)
r = 0·892
Log$_e$ $\overline{L}$r (var. log$_e$ Lr) = 1·559 (0·060)
Log$_e$ $\overline{Th}$r (var. log$_e$ Thr) = 0·169 (0·109)
r_e = 0·907
α (var.) = 1·348 (0·01146)

$\overline{L}$ mm. (var.) = 6·00 (4·096)
$\overline{W}$ mm. (var.) = 7·13 (5·335)
r = 0·968
a (var.) = 1·142 (0·00293)

TABLE 24. Statistics of length (L), maximum width (W), thickness (Th), length of rugate region (Lr), and thickness of rugate region (Thr) of 30 shells or pedicle valves of *E.* (*Eomarginiferina*) *trispina* sp. n.

Subfamily **ECHINOCONCHINAE** Stehli 1954

Genus ***ECHINOCONCHUS*** Weller 1914

Echinoconchus cf. ***punctatus*** (J. Sowerby)

(Pl. 17, figs. 11–15 ; Pl. 18, figs. 1–4)

Material. Few fragmentary remains from the Bunnahone locality near Derrygonnelly, Co. Fermanagh. D_1.

Measurements (in mm.)

	length	width
Young pedicle valve (BB.52936)	—	15·5
Incomplete brachial valve (BB.52938)	1·6	—
Incomplete brachial valve (BB.52939)	*c.* 24·0	*c.* 29·0

Description. *Echinoconchus* is insufficiently represented in the faunas to allow a full description, but a few young valves identified as *Echinoconchus cf. punctatus* (J. Sowerby) are represented. The fragments are typical of the subfamily in having concentrically arranged bands of recumbent spines of more than one diameter. The spines are concentrated on anteriorly sublamellose rugae. The spines occur in up to 5 ranks in each concentric band and when all are preserved they form a dense anteriorly directed comb in which the lower, more anteriorly placed, spines are more slender. This feature, together with almost flat brachial valve and its interior, distinguishes the young valves of *Echinoconchus* from those of *Krotovia lamellosa* sp. n., with which it occurs in the Fermanagh faunas.

The dorsal interiors are described by Thomas (1914) and by Muir-Wood & Cooper (1960) as having lateral ridges that continue along the hinge margin. In the Fermanagh valves the lateral ridges diverge from the hinge margin and merge laterally into indistinct ridges formed at the interspace of two external rugae (Pl. 17, fig. 13). There are no interiors amongst Sowerby's original specimens, so while the descriptions of the above authors is probably inaccurate for young specimens, this difference may result only from the juvenile nature of the Fermanagh material in which secondary shell deposition along the hinge margin had not taken place. (A similar ontogenetic change occurred in *Plicatifera plicatilis*.)

Genus ***PUSTULA*** Thomas 1914

Pustula cf. ***pyxidiformis*** (de Koninck)

(Pl. 18, figs. 5–14 ; Pl. 19, figs. 1, 2)

Measurements (in mm.)

	length	width
Incomplete pedicle valve (BB.52940)	36·0	—
Incomplete shell (BB.52941)	*c.* 33·0	*c.* 45·0
Incomplete shell (BB.52942)	*c.* 43·0	*c.* 60·0
Incomplete brachial valve (BB.52943)	31·4	42·5

The genus is poorly represented in the Bunnahone fauna by a few incomplete large specimens, and no young valves were found. For this reason a full description has not been attempted and the specimens are only tentatively assigned.

These shells, whigh are large for the fauna, are more or less plano-convex when adult ; there is a short antero-dorsally directed trail and the pedicle valve is slightly medianly sulcate. The ornamentation is distinctive, consisting of poorly developed rugae, becoming sublamellose anteriorly, from between which more or less radially arranged prostrate spines arise from elongate spine bases having an irregular quincuncial pattern. The pedicle valve interior for *Pustula* was not described by Muir-Wood & Cooper (1960), so the available valve is noteworthy (Pl. 18, figs. 5–7). The muscle field extends about two-thirds of the valve length (measured as a chord to the valve's curvature) and is clearly divisible into raised central adductor scars and flanking, longitudinally striated, elongately trigonal diductor scars. The median sulcation occurs most prominently in the anterior region of, and just anterior to, the adductor platform. The brachial valve has a short postero-dorsally directed cardinal process with trifid external surface, as a result of fusion of the median muscle boundaries. Internally it is supported by the low posterior end of the median septum and a pair of well developed lateral ridges that diverge from the hinge-line at about 10° and extend for about three-quarters of the hinge width. The muscle and brachial impressions are obscure or lacking in the present material, but are poorly known from specimens of other areas.

The taxonomic position of these Fermanagh specimens is in doubt as their dorsal interiors are more comparable to the American genus *Stegacanthia*, as illustrated by Muir-Wood & Cooper (1960, pl. 48, fig. 12), than to *Pustula* (pl. 84, fig. 4) from the British Isles. For the present and until further material can be collected from Ireland and compared with American species, the Fermanagh shells are questionably assigned to *P. pyxidiformis* solely by reason of their comparable external ornamentation. The ornamentation of the holotype of *Pustula pustulosa* (B.M.N.H. no. B.419) is of more discrete pustule-like spine bases confined to indistinct rugae, and only anteriorly do these spine bases become somewhat elongate, as is typically seen on *P. pyxidiformis* and *Stegacanthia bowsheri*.

Family **DICTYOCLOSTIDAE** Stehli 1954

Genus ***ANTIQUATONIA*** Miloradovich 1945

Antiquatonia sp.

(Pl. 17, figs. 1–10)

A well preserved incomplete pedicle valve, together with a few fragments of other pedicle valves from the Bunnahone locality, clearly show the characteristics of *Antiquatonia*. Brachial valves are not known for certain, but the fragment illustrated (Pl. 17, figs. 7–10), together with three other similar cardinalia, are thought to belong to the genus.

MEASUREMENTS (in mm.)	length	width
Incomplete pedicle valve (BB.52934)	25	*c.* 39

About 20 rugae are developed over the postero-ventral part of the pedicle valve but the anterior 4 or 5 are not persistent and die out across the slightly sulcate median region. The ribbing is well developed with about 6 ribs occurring in 2·5 mm., 5 mm. antero-medianly of the ventral umbo. The ribs continue on the trail but are not of uniform width, possibly as a result of spine-growth interference. Two pairs of prominent rows of spines are developed ; one pair extending from near the umbo towards the postero-lateral margins, at a narrow angle to the hinge-line ; the other pair developed along the flanks, just below the groove that separates the ears from the flanks, and arose from a low ridge.

Internally the " rarely developed transverse ridges across the ears " (Muir-Wood & Cooper 1960 : 270) are present, as are the dendritic raised adductor scars and flabellate longitudinally striated diductor scars. Anterior to these, and covering the remainder of the inferred visceral cavity, are irregular ridges comparable to those observed in *E. Eomaginiferina* subgen. nov. (Pl. 17, fig. 3).

The fragment of brachial valve appears to be comparable to that known for *Antiquatonia*. The cardinal process is sessile and trifid, by the complete fusion of the median muscle boundary ridges, and each myophore is deeply incised. The lateral ridges do not appear to diverge from the hinge-line of the available specimens. The median septum is low and broad posteriorly, supporting the cardinal process, but between the adductor scars is poorly developed and anteriorly it is high and blade-like.

Family **LINOPRODUCTIDAE** Stehli 1954

Genus ***OVATIA*** Muir-Wood & Cooper 1960

Ovatia sp.

(Pl. 19, figs. 3–10)

A few silicified shells from the Bunnahone locality are ascribed to *Ovatia* although the genus was previously unrecorded from the British Isles (Muir-Wood & Cooper 1960 : 314). The remains are of young valves but indicate a subcircular outline, and the most prominent external ornamenation is of fine radial ribbing developed over both valves ; there being about 8 ribs in 2·5 mm., 5 mm. from either umbo. Costellae seem to be added by dichotomous branching on the brachial valve and by intercalation on the pedicle valve. Spines are developed from the ribs, expecially posteriorly (Pl. 19, fig. 10), and a small pedicle sheath was most probably present during early life. An indistinct rugation is most clearly developed laterally and posteriorly, near the straight hinge-line. The cardinal process is sessile and quadrifid, although the two median muscle boundaries are only narrowly separated (Pl. 19, fig. 4) and might well appear fused, giving a trifid process, in less well preserved material. Internally the median muscle boundaries extend beyond the lateral muscle boundaries and the cardinal process is supported by both the lateral ridges and a broad low median septum which becomes narrow and high anteriorly.

Measurements (in mm.)

	length	width
Incomplete pedicle valve (BB.52945)	c.6·0	7·4
Incomplete pedicle valve (BB.52946)	—	c. 8·0
Incomplete brachial valve (BB.52947)	c. 11·5	—

Although similar, *Cancrinella* Fredericks is more clearly rugate and the pedicle valve is more spinose, while *Linoproductus* Chao has a rather different dorsal interior. Both these species are restricted to Upper Carboniferous and Permian rocks by Muir-Wood & Cooper (1960 : 298, 302). It seems possible that the Fermanagh shells represent the young of forms precursory to true linoproductids of higher strata and that older rocks, down to the Ballyshannon Limestone, contain species of *Ovatia* or *Balakhonia* and not *Linoproductus* as commonly described in the past.

Recently Sarycheva (1963 : 231) described her new genus *Balakhonia* from the Visean to Namurian of the Kuznetsk Basin. This genus was erected for species commonly attributed to *Linoproductus*, but which differ internally and in having thin shells and a narrow body cavity. The cardinal process is described as being small and bilobed, the two lobes being separated and not fused medianly, as they are in the heavy trifid cardinal process of *Linoproductus*. Spines are neither prominent nor frequent on the pedicle valve. Sarycheva says that her genus is similar to *Ovatia*, but separates the two by reason of *Ovatia's* smaller size, trifid cardinal process (the description of Muir-Wood & Cooper 1960) and its short lateral ridges. Such differences could be attributed to the smaller size and less developed morphology of *Ovatia*, provided that the cardinal process is more similar than was envisaged by Sarycheva. If the genera are distinctive it is likely that *Balakhonia* may usefully receive some of the British Lower Carboniferous species, but until specimens or better illustrations are available of the Russian genus, the Fermanagh material is tentatively assigned to *Ovatia*.

Family **PRODUCTELLIDAE** Schuchert & Le Vene 1929

Chonopectinid sp.

(Pl. 19, figs. 11–16)

Measurements (in mm.)

	length	width
Complete brachial valve (BB.52948)	7·1	12·4
Incomplete brachial valve (BB.52949)	7·6	—

This material consists of about a dozen complete or incomplete brachial valves of doubtful systematic position and with no known matching pedicle valves. These brachial valves are subrectangular in outline, a little over one-half as long as wide, with a straight hinge-line commonly forming the widest part of the valve ; they are flat to gently concave in profile, but irregular, and the ornamentation of concentric sublamellose rugae is irregular and usually distorted as if by close contact with some foreign object, such as a fenestellid colony. The hypercline interarea is short and extends almost the full hinge width ; the notothyrium is filled by the base of the cardinal process and narrow dorsal ends of the sockets. The cardinal process is bilobed, quadrifid and perpendicular to the commissural plane, its myophores are posteriorly directed and the two lobes are only narrowly separated. The cardinal process is supported by a low short median septum extending about one-quarter of the valve length, and by short socket ridges that tend to recurve to the interarea. The interior is otherwise devoid of markings, save for a representation of the external ornamentation.

The short interarea and presence of sockets indicates that the shells possessed teeth, and the pedicle valve was probably convex to allow for the body cavity. The Fermanagh valves match a single brachial valve (B.53687) collected from Thorpe Cloud, Derbyshire, which is amongst specimens of *Chonetipustula carringtoniana*. However, it is quite distinct from that species and could only doubtfully be assigned to *Chonetipustula* because of its thickened shell and cardinal process which is more reminiscent of the strophalosids. *Chonetipustula* has been placed in the subfamily Chonopectinae by Muir-Wood & Cooper (1960). At the same time these authors erected a new genus, *Quadratia*, with *Productus hirsutiformis* Walcott as type species. This genus has similarities to the present material, but apparently has a less well defined rugation and is internally tuberculate.

Thus, although the cardinal process is strophalosiid in nature, the general outline and characters as yet known are suggestive of the species belonging to the Chonopectinae. However, the specimens cannot be assigned to any of the genera yet described.

The description of this material has been given last because of its doubtful systematic position, but the author agrees with Muir-Wood in considering the productellinids to display primitive features within the Productacea.

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